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PERMINERALIZED PLANTS FROM THE EOCENE, ALLENBY

FORMATION OF SOUTHERN BRITISH COLUMBIA

by

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A THESIS

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Permineralized Plants from the Eocene, Allenby Formation of Southern British Columbia", submitted by James Frederick Basinger in partial fulfilment of the requirements for the degree of Master of Science.

ABSTRACT

Mass collections from the Ashnola locality, near Princeton, British Columbia, have revealed a far more extensive and diverse flora than previously recognized. Plant parts have been permineralized with silicates and are found in an outcrop of interbedded chert and coal. The age of the Ashnola locality is established as Middle Eocene on the basis of numerous K-Ar dates from associated strata and palynological data.

A comparison of the Ashnola locality with other permineralization localities establishes the Ashnola flora as one of the most diverse assemblages of well-preserved permineralized plants yet discovered in the early Tertiary. Pinus arnoldii, P. similkameenensis, and a semiaquatic dicotyledon, Eorhiza arnoldii, which have been described previously by Miller (1973) and Robison and Person (1973), are re-examined. The present study includes brief descriptions of three ferns including Dennstaedtiopsis aerenchymata, taxodioid reproductive and vegetative remains assignable to Metasequoia, pollen cones of the genus Pinus, and leaf remains of sabaloid palms. A report of diverse reproductive and vegetative angiospermous organs is also included. Of greatest interest are numerous flowers whose fine preservation allows assignment not only to the Rosaceae, but to specific tribes within the family. This is the earliest record of rosaceous floral anatomy and provides valuable information on evolution within the Rosaceae.

The Ashnola flora is similar to compression localities in the area in containing a combination of temperate and subtropical elements. Reasons for this mixing are proposed and the confusion that this assemblage has introduced into early attempts at age determinations is reviewed.

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CHAPTER 1

INTRODUCTION

Material from the Ashnola locality was mass collected
during the summers of 1974 and 1975 and has yielded large
quantities of permineralized megafossils. The locality is
found on the east bank of the Similkameen River approximately
5 miles south of Princeton, southern British Columbia, and
forms an outcrop of interbedded chert and coal that extends
across the river to form a partial dike. The plants are
permineralized with, and are found embedded in, the silicates
which form the cherty layers. Although the age of the Allenby
Formation, of which the Ashnola locality is a part, has been
questioned in the past, recent evidence indicates a Middle
Eocene age.

Compressed megafossils and dispersed palynomorphs are
common in Tertiary sediments and provide information about
external morphology and paleofloristics, but they can con-
tribute little to our understanding of internal anatomy,
organ development, or reproductive mechanisms of Tertiary
plants. By contrast, permineralized plants showing internal
structure can provide this latter information. Permineraliza-
tion fossils are, however, quite uncommon in the Tertiary and,
with the exception of permineralized wood, only a few specimens
have been found at any one locality. It will be seen that the
Ashnola locality contains the most diverse flora of well-
preserved, permineralized megafossils yet discovered in the
early Tertiary.

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Only in the last 10 years has the potential of the Ashnola locality been recognized. Unlike most highly productive megafossil localities, the locality went unnoticed by amateur collectors, largely because the fossils are not immediately obvious on the chert surface and are virtually impossible to detect on a freshly broken and unweathered face. If not cut and treated with hydrofluoric acid to reveal the entombed plants, the blocks of chert are anything but aesthetically pleasing.

Arnold and Boneham were first to exploit the Ashnola locality and a palynological study was made by Boneham (1968). Material from their collection was made available to Miller (1973), who described Pinus arnoldii and Pinus similkameenensis, and to Robison and Person (1973), who described a semi-aquatic dicotyledon called Eorhiza arnoldii. These authors also reported the presence of two or three ferns including Dennstaedtiopsis aerenchymata Arnold and Daugherty (1964), dicot stems, an ascomycete fungus, fragments of one or more moss gametophytes, and a few seeds of unknown affinity. The diversity found during the present study has, however, far exceeded that previously recognized.

The primary objective of this thesis is to present an account of this diversity and to present detailed reports of some of the more conspicuous elements of the flora. Included in these reports are male cones of the Taxodiaceae and Pinaceae, fern rhizomes and petioles, and petioles and lamina of a sabaloid palm. Of greatest interest were numerous flowers whose preservation is fine enough to allow

an assignment to not only the Rosaceae, but to specific
tribes within the family. This is the earliest known
record of rosaceous floral structure and has provided
valuable information on floral evolution within the Rosaceae.

Paleoecology will be discussed in reference to both the
florule of the Ashnola locality and to the flora of the
Allenby Formation in general. Subtropical forms such as
the sabaloid palms which are the first palms reported from
the Allenby Formation, together with pines and other temp-
erate forms show a complex mixing of northern (Arcto-
Tertiary) and southern (Neotropical-Tertiary) elements of
the flora of Eocene North America. Causes of this mixing
will be explored and the confusion that the resulting
assemblage introduced into early attempts at age determina-
tion of the Allenby Formation will be reviewed.

Tertiary Fossil Remains

Fossil remains of Tertiary vegetation occur primarily
as compressed megafossils and dispersed palynomorphs.
Although these fossils provide us with information on
external morphology and paleofloristics, they reveal little
of internal structure or reproductive mechanisms.

Our understanding of evolutionary relationships among
plants is based primarily upon characteristics of reproduc-
tive structures and development and to a lesser degree on
vegetative characteristics. Our modern schemes of class-
ification are constructed by evaluating these characteristics.

Because the more delicate and somewhat ephemeral reproductive organs are seldom found in the compressed state, classifications based on fossil genera have been constructed primarily on vegetative features. As we know it is very difficult to accurately assign a taxonomic position to living genera unless both vegetative and reproductive organs are known. This difficulty is compounded for fossil plant remains because of the fragmentary, often incomplete nature of the fossil record and the fact that different plant structures for a given genus may evolve at different rates. Christophel emphasized this latter point when he stated (1973, p. 26):

> "... the similarity of a fossil leaf (or other plant organ) to an extant counterpart does not, indeed cannot, be taken as evidence that the entire extinct and extant organisms are identical (at the generic level). To do so denies the paleobotanically proven fact that different plant structures evolve at different rates in certain organisms and negates the possibility that the majority of the organs of a given plant may have evolved into generic uniqueness in a given number of million years while one organ remained unchanged."

An example of differing rates of evolution can be found in the Juglandaceae of the lower Tertiary, where leaves of the genera Juglans and Carya were found attached to very similar reproductive organs (Chaney, 1949b). Although these two genera were differentiated vegetatively by the Eocene, distinct reproductive morphology had not yet appeared. On the other hand pollen grains and fruits of Engelmannia are common in lower Tertiary sediments, but leaves of this genus have not been recognized from these same strata (Dilcher, (1973). It is apparent that reproductive organs of Engelmannia had evolved by the early Tertiary, but leaf

structure had not yet changed to its present state.

The examples given show that this approach applies to both isolated reproductive and vegetative organs. However, since modern systems of classifications are principally derived from reproductive characters, conclusions of taxonomic affinity are more reliable if based on reproductive organs.

The adoption of this philosophy expressed by Christophel leads one to restrict the application of modern generic names to those fossil plants that are quite well known vegetatively and reproductively. Isolated organs are assigned to form- and organ-genera. This allows for the classification of isolated organs without creating the erroneous impression that a modern genus, with all of its characteristics, existed at some time in the past.

Workers such as Berry (1916, 1924), Knowlton (1902, 1922), Hollick (1930, 1936), and Bell (1949) had not accepted such a view and assigned modern generic names to vegetative remains, particularly those of leaves, on the basis of gross structural similarities. Among other misconceptions, this approach resulted in a belief that Cretaceous and lower Tertiary floras contained high percentages of apparently highly evolved angiosperms. Recent work by Wolfe (1969), Hickey (1973), and Dilcher (1973, 1974) has largely dispelled this belief, for they have been able to show that large numbers of plant megafossils were misidentified by the early workers. Although workers such as Dilcher, Wolfe, and Hickey have been able to eliminate many of the problems

arising from the assignment of modern generic names to incompletely known fossil plants based on vegetative remains, there still exists the problem of properly interpreting these vegetative remains in the absence of evidence from reproductive structures. Even if artificial classification schemes based on leaf structure are constructed, the uncertainty of the position of the extinct genera in natural systems of classification remains, as long as little or nothing is known of their reproductive characteristics.

Unlike compressed megafossils, permineralized (petrified) plants are able to provide information about internal structure and reproductive morphology. Permineralized specimens often reveal many delicate vegetative and reproductive organs of both woody and herbaceous plants showing superb structural detail. This is due in part to conditions present at the time of deposition. The Ashnola chert, like the Rhynie chert, American coal balls, and the Deccan Intertrappean cherts, was probably deposited in a very still water environment (see Locality-Formation). This type of depositional environment would allow an accumulation of more delicate plant parts in addition to more resistant organs. The permineralization of the accumulated debris effectively protects the more delicate plant parts from destruction by compression. Thus, they not only accumulate intact, but are retained in a recognizable state after fossilization. Only in permineralized plants are detailed anatomical studies possible. The gradual accumulation of plant organs also permits the preservation of many develop-

mental stages of those organs, which provides an opportunity for developmental studies.

The fact that so few Tertiary petrifaction localities are known makes work in this area of critical interest. Since nearly all knowledge of Tertiary vegetation has been derived from compressed megafossils, exceedingly little is known of reproductive characteristics and the internal structure of these plants. The Ashnola chert has great potential in this area because of the great diversity of petrified reproductive and vegetative structures. Unfortunately, the rarity of Tertiary permineralized plants, in addition to the lack of knowledge in comparative anatomy of living plants, makes the study of material such as the Ashnola chert very difficult. It is also difficult to make comparisons of permineralized and compressed organs. External morphology is not immediately available in the former, while anatomical detail is unavailable in the latter.

The compilation of information from other Tertiary localities containing petrified plants which follows emphasizes that permineralized plants in the Tertiary are exceedingly rare and that little is presently known about them. The fact that so little information has been obtained from Tertiary plants preserved as petrifactions places the Ashnola chert in a position of considerable importance.

Tertiary Permineralization Localities

Considering the great value of permineralized plants,

it is very unfortunate that so few localities have been discovered in Tertiary starta. With the exception of petrified wood, which occurs frequently in the Tertiary as isolated fragments, rarely more than a few specimens are reported from a single locality.

Permineralized lignite or degraded peat, such as that described by Ting (1972) from the Paleocene of North Dakota, has been found, but preservation is less than ideal due to degradation prior to preservation. Ting described the preservation as "comparable to that of Carboniferous coal balls" and that it was "the first reported finding of such material in North America". Unfortunately, the silicified peat is not extensive, for the material occurred as a lens only 15 cm. thick and 1 m. long. This cannot be compared to the extent of the Ashnola locality, where over 3 tons of material have been recovered to date without effecting any appreciable change in the outcrop. It is also apparent, from photographs of the North Dakota material (Ting, 1972, p. 165), that superior preservation is found in the Ashnola chert. Preservation, however, is sufficiently good in Ting's material to identify roots, wood fragments, fern sporangia, and seeds.

An assemblage of structurally preserved roots from a permineralized soil was described by Wheeler (1972) as part of the Miocene Taper Hill Flora of Colorado. Apparently there was little else recognizable within the nodules.

One of the more interesting fossil localities is the

nut beds of the London Clay, which have been thoroughly described by Ried and Chandler in 1933. The seeds and fruits of the London Clay flora, which make up the largest component of the assemblage, have been permineralized with iron pyrites and occur in marine sediments. Ried and Chandler explained the formation of the beds by the rafting of vegetation from rivers into the sea, where different types of organs would become waterlogged, sink, and become concentrated at various distances from shore. External morphology and gross structure are readily seen in these fossils, but there is a lack of vegetative material with which to associate them. This is a reversal of the kind of problem often found in compressions. There is also a lack of developmental stages present, for essentially all seeds and fruits found were mature.

Plant-containing nodules have been described from Japan by Stopes and Fujii (1911). The nodules are also found in marine sediments and may have been formed in a manner similar to that of the London Clay deposits, but contain a greater variety of plant organs than the London Clay beds. Discoveries from this locality include the gynoecium of a flower that was described by Stopes (1910) as possibly liliaceous. The Japanese material is limited both in quantity and in the quality of preservation.

The nut beds of the Eocene, Clarno Formation of Oregon may be classified as casts and molds rather than permineralized fossils. Scott (1954), however, found some degree of

structure visible. These nut beds may have been formed by
rafting as were the London Clay nut beds, but a basic
difference is the formation of the Clarno nut beds in a
lacustrine environment.

The chert beds of the Deccan Intertrappean Series of
India are quite comparable to those of the Ashnola locality
in both structure and age and, until the present study, con-
tained the most extensive petrifaction floras known in the
Tertiary. It is felt that a detailed description of the
Indian material is required if floral comparisons with the
Ashnola material are to be attempted.

The Deccan Intertrappean Series

The Deccan Intertrappean Series of India represents
perhaps the best known of Tertiary permineralization floras.
The Deccan Traps are an extensive series of volcanics that
cover an area of more than 200,000 square miles with a
maximum thickness of about 2100 meters (Rao, 1936). Thin
sedimentary layers are found between successive lava flows
of the Lower (about 450 meters) and Upper (about 150 meters)
Traps and are called the Lower and Upper Intertrappean Series
respectively (Blanford, 1867; Rao, 1936). The Middle Traps
(about 1200 meters) are devoid of Intertrappeans.

The Intertrappeans were formed in hollows on the lava
sheets and contain lacustrine or marsh deposits, and the
nature of the fossil remains reflects this type of deposi-
tional environment. These sedimentary beds are not large,

each having a lateral extent of no more than three to four miles and a thickness of ½ to 3 meters (Prakash, 1960; Lakhanpal, 1970b).

Early workers such as Malcolmson (1837), Hislop and Hunter (1855), and Oldham (1871) concluded that the Traps were of an early Tertiary age, basing their conclusions on fossil evidence. Although an Upper Cretaceous age was later proposed on the basis of stratigraphic correlation with associated Mesozoic strata (Medlicott and Blanford, 1879; Wadia, 1919; Holland, 1926), recent work has supported an early Tertiary (Eocene) age for the Lower Traps (Woodward, 1908; Sahni, 1934, 1941; Sahni and Rode, 1934, 1943; Rao, 1935; Crookshank et al, 1937; Rao and Rao, 1939; Prakash, 1960; Lakhanpal, 1970a).

The flora of the Upper Intertrappeans is less extensive and less well known than that of the Lower Intertrappeans. Rao (1936) believed that the differences between the floras of the Upper and Lower Intertrappeans and the extent of the lava flows comprising the Traps indicate a Miocene age for the Upper Intertrappeans.

The flora of the Deccan Intertrappeans is very rich and varied, with almost 200 species reported to date. It must be remembered, however, that the Traps are extensive beds and extend through considerable time as well as space. The large number of localities with a variety of species is, to a great degree, responsible for the diversity. In addition to elements of space and time, ecological factors have

resulted in considerable differences among the individual florules, adding to the diversity of the composite flora. At Rajahmundry, plant remains are exclusively aquatic and consist basically of _Chara_ and other algal forms indicative of estuarine conditions (Pia, Rao, and Rao, 1937a,b; Rao and Rao, 1939; Rao and Rao, 1940). Aquatics are also found at Sausar, but unlike Rajahmundry, the flora has the aspect of fresh water lakes or marshes. Included in the flora are charophytes and other algae (Sahni and Rao, 1943), _Azolla_ (Sahni, 1941), and some other pteridophytes (Lakhanpal, 1970b). The richest of all known localities in the Deccan Intertrappeans is that of Mohgaon Kalan. This locality appears to represent an ancient marsh that contains, in addition to aquatics such as algae, bryophytes, and water-ferns, conifers, dicots, and monocots of which there is a predominance of palms. Comprehensive lists of species from Mohgaon Kalan, as well as from all other known localities in the Deccan Intertrappeans, can be found in Sahni (1931), Prakash (1960), Lakhanpal (1970b), and Rao and Achuthan (1971). These three localities, Rajahmundry, Sausar, and Mohgaon Kalan, have yielded an abundance of good material, but material from the numerous other localities rarely consists of more than a handful of specimens.

Considering both spacial and temporal differences, as well as differences in habitat and floral composition among localities, it does not seem reasonable to support the proposition of a single massive flora. Individual localities

appear to have their own unique floras, and should be treated as such and not collectively (Lakhanpal, 1970b).

If identifications of specimens from the Intertrappeans are correct, then the fossil floras apparently had much the same aspect as do the modern floras of that region and of tropical South America (Prakash, 1960; Lakhanpal, 1970b). The presence of Nipa (Sahni and Rode, 1937; Chitaley, 1960), Musa (Jain, 1964a,b) and Heliconiaites (Trivedi and Verma, 1972) of the Musaceae, and certain palms indicates a tropical climate (Lakhanpal, 1970b). Petrified woods lack distinct seasonal growth rings as well. There are some more temperate forms such as Sparganium found in the fossil floras (Lakhanpal, 1970b), but their presence has not yet been explained.

At both the Rajamundry and Sausar localities are found basically aquatic forms such as algae; therefore, neither compares favorably to the Ashnola locality which is composed primarily of vascular plants which grew adjacent to the depositional area. The depositional environment of the Ashnola locality compares most favorably, then, to the Mohgaon Kalan locality. Mohgaon Kalan is also the only Intertrappean locality that can be considered comparable to the Ashnola locality in degree of diversity and quality of preservation. However, a direct comparison of plants found in the two localities is impossible, for the flora of Ashnola, as will be seen, is composed primarily of warm temperate to subtropical forms which show no similarity to the basically tropical elements of Mohgaon Kalan.

The Clarno Chert

The Clarno chert of Oregon is found in the Middle
Eocene, Clarno Formation and is relatively similar in
appearance to the Ashnola chert. There is some basis for
believing that both the Clarno and Ashnola chert beds are
in some way related (see Geology-Locality). The Clarno and
Green River Formations have long been known to contain an
abundance of silicified wood as well as fern stems (Arnold,
1945, 1952). Arnold and Daugherty (1963, 1964) were first
to report on the Clarno chert, which was found below a
lava sheet and above a 130-meter thick ash bed. The chert
is light grey, a color imparted by quantities of ash within
the matrix, and forms a bed less than one meter thick. As
a result of their study, two ferns were described from the
chert, Acrostichum preaureum (Arnold and Daugherty, 1963)
and Dennstaedtiopsis aerenchymata (Arnold and Daugherty,
1964). These two reports also note the presence of Equisetum,
twigs of herbaceous and woody dicotyledons, wood of Ginkgo,
and numerous palynomorphs. Equisetum clarnoi was recently
described from the locality by Brown (1975). The Clarno
chert was the first petrifaction locality containing an
abundance of well-preserved herbaceous plants to be found
in the Tertiary of North America. As yet, however, the
diversity of the flora has not been proven great.

Permineralized plants of the Tertiary have, due to
their rarity, offered little to our understanding of Tertiary
vegetation. This is unlike the Carboniferous, where much

of our knowledge of Upper Paleozoic plant structure, both vegetative and reproductive, is based on the coal-ball floras. The value of the information derived from these Paleozoic petrifaction floras is quite apparent. It is expected, then, that the discovery and investigation of such floras in the Tertiary could likewise contribute a wealth of knowledge of Cenozoic plant structure and reproductive mechanisms.

The Ashnola Locality

The Ashnola locality is the first locality found in North America that offers an extensive survey of permineralized Tertiary plants. All other Tertiary permineralized beds located in North America are limited by the quality of preservation, the abundance of material, or the diversity of the flora. In these respects, the Ashnola chert is rivaled only by the cherts of the Deccan Intertrappean Series.

The Ashnola locality was first described by Boneham (1968), who reported the presence of pine cones and needles and rhizomes of Dennstaedtiopsis aerenchymata Arnold and Dautherty (1964). The pine cones and needles were described by Miller (1973) as Pinus arnoldii and P. similkameenensis, respectively. A semiaquatic dicotyledonous rhizome, Eorhiza arnoldii, was described at the same time by Robison and Person (1973). These same reports indicate the presence of woody stems of two or more dicots, ferns, bryophyte remains, unidentified seeds, and an ascomycete fungus. The diversity

found in the present study is much greater than previously
suspected. In both abundance of material and quality of
preservation, the Ashnola locality is comparable to the
best coal-ball localities of the Carboniferous, and it is
possible that the Ashnola locality will provide an under-
standing of Tertiary fossil floras in a way that some coal-
ball localities have helped in our understanding of
Carboniferous floras.

CHAPTER 2
GEOGRAPHY and GEOLOGY

Geography

The Ashnola locality is found on the east bank of the Similkameen River approximately 5 miles S.S.W. of the town of Princeton, British Columbia. The locality is slightly more than 2 miles S.S.W. of the abandoned town of Allenby and almost directly across the river from the abandoned mining camp of Ashnola (Princeton Map Sheet 92 H/7 1:50,000 U.T.M. Grid Ref. 783 724). Boneham (1968) referred to this as locality "I" during his palynological studies, but it is here named the Ashnola locality (see Fig. 1).

The town of Princeton is found to be at the approximate center of a small, natural basin which contains a considerable thickness of sedimentary rocks (see Geology). These sediments were determined by Camsell (1907) to extend approximately 14 miles north to south and from $3\frac{1}{2}$ to 5 miles east to west. The Ashnola locality is found near the southern limit of the sediments. The soft nature of the Tertiary deposits as opposed to the very resistant Triassic volcanics which surround and underlie the basin provides for an abrupt topographic change upon entering the Princeton basin. Dawson (1879, p. 49B) described this change as he entered the basin from the southwest:

> "These (Mesozoic volcanics) are now succeeded by softer igneous and sedimentary beds of the Tertiary, and the whole aspect of the country at the same time

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Fig. 1.   Map of the Princeton area showing the Ashnola
          locality in relation to the Tertiary sediments
          of the Princeton basin and local geographic
          features.   (After Shaw, 1952)

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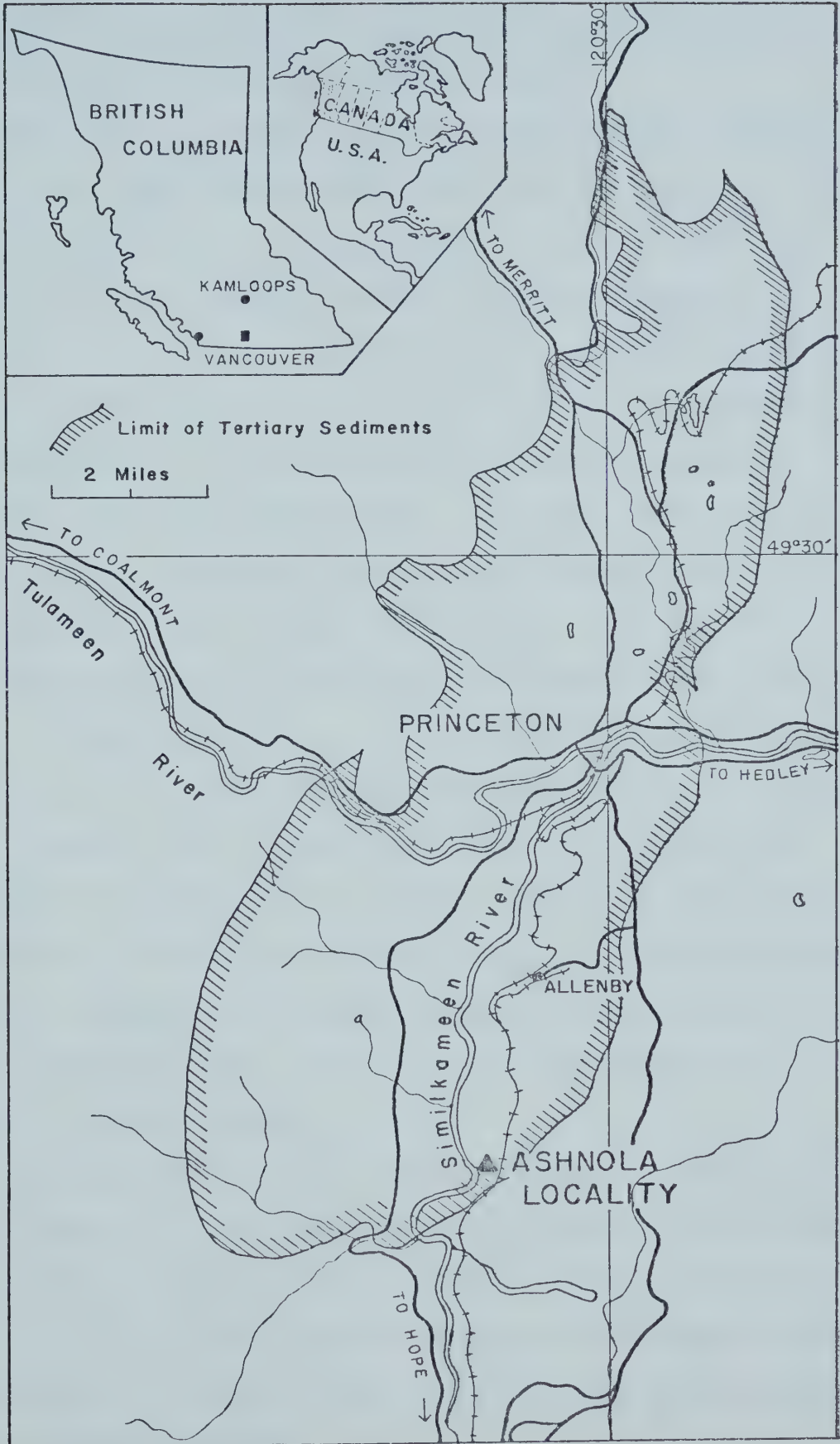
changes for the better. The valley widens, and the brook (Whipsaw Creek) cuts rapidly down to a lower level, running between high terraced banks with occasional cliffs of volcanic rocks."

There are no volcanic cliffs at the Ashnola locality, but here the Similkameen River does flow at the foot of a steep embankment on the eastern side of the broad, deep valley cut by the river. On the west bank, opposite the locality, is a flat and open field, now used for agricultural purposes, that probably represents earlier river channels and flood plain. The Ashnola chert is apparently more resistant than most other rocks in the area, for it forms a partial dike across the river while surrounding strata have long since been eroded by the water (see Fig. 2).

Although there is little glacial drift at the Ashnola locality, large quantities of the material blanket most of the area, and solid rock is usually only exposed by stream cuts. Camsell (1907) notes that this drift imparts "an appearance of fairly mature erosion, giving to the hills in the belt a rounded and graded outline", a characteristic that is a conspicuous feature of the Interior Plateau of British Columbia, onto which the Princeton basin abuts along its northern margin.

The Princeton basin is found between two forks of the Cascade Range and is contained on the west and south by the true Cascades (including the Hozameen and Hope Mountains), and on the east by the eastern Cascades or Okanagan Range. To the north, the country opens out into the Great Interior Plateau (Camsell, 1907).

Fig. 2.   View of the Ashnola locality looking northwest
          from the east bank of the Similkameen River.   The
          outcrop of interbedded chert and coal extends into the
          river to form a partial dike.

The elevation of the Ashnola locality is slightly more than 700 meters, which is about 100 meters above the townsite of Princeton. The nearby hills approach 1300 meters, and altitude gradually increases to the south, east, and west.

Geology

The first geological studies of south-central British Columbia were made by Bauerman in 1859-1861, although this work was not published until 1884. Bauerman recognized the presence of Tertiary deposits in a number of the natural basins of the area. Among these were the deposits of the Princeton area, or Vermilion Forks as it was known at that time.

A later study, although published before that of Bauerman, was completed by Dawson (1879). Unlike Bauerman, Dawson showed considerable interest in the Tertiary basins and has provided a detailed report on the geology of the Princeton area.

Camsell (1907, 1915) considerably extended the study begun by Bauerman and Dawson. Camsell attempted to give a history of the formation of the Princeton basin as well as a description of the present structure. Later studies were made by Rice (1947), Shaw (1952), and Hills (1962, 1965a,b).

The Tertiary deposits of the Princeton basin lie unconformably on the Triassic volcanics of the Nicola Group, named by Dawson in 1879. The Nicola Group is also found to underlie a number of other Tertiary basins in the area such

as the Tulameen and Merritt basins (Dawson, 1879; Boneham, 1968). These Triassic basement rocks have suffered distortion and severe erosion, likely due to uplift during the Upper Cretaceous (Camsell, 1907; Shaw, 1952). Some sediments of a Lower Cretaceous age are present in the vicinity of the Princeton basin, but there appears to have been no deposition of sedimentary rocks in the area during the Upper Cretaceous.

Regional subsidence must have occurred during the early Tertiary to create the many basins of the area which now contain deposits of this age. This explanation accounts for the volcanism at the beginning of this period and for the great thickness of the deposits in a basin such as the Princeton, where there are possibly 2500 meters of beds. Other possible causes such as valley damming by lava flows cannot account for such a thickness of beds (Shaw, 1952) . The early Tertiary sediments have since been folded and faulted, with dips ranging from 10° to 45°. This is probably a result of uplift responsible for the creation of the Cascade Mountains during the late Tertiary.

Both volcanic and sedimentary beds were recognized as part of the Tertiary deposits of the Princeton basin by Dawson (1879) and Camsell (1907). Rice (1947) described the Princeton lavas as forming the bulk of the Tertiary deposits and as existing both above and below the sedimentary beds. Shaw (1952) first gave a fairly detailed description of the deposits and recognized three formations within the Princeton basin. They were, in ascending order, the Lower

Volcanic Formation (1400 meters thick), the Allenby Formation (1100 meters thick), named after an outcrop near the town of Allenby, and the Upper Volcanic Formation (150 meters thick) (see Fig. 3).

The Tertiary sediments, the Allenby Formation, cover an area of approximately 40 square miles, extending about 14 miles north to south and $3\frac{1}{2}$ to 5 miles east to west. The Ashnola locality, as noted in the previous chapter, lies near the southern limits of the Allenby Formation. Boneham (1968) was the first to study the Ashnola locality and determined its stratigraphic position as 550 meters above the Princeton-Black coal seam, or about 850 meters above the base of the Allenby Formation.

That the Ashnola locality is a part of the Allenby Formation, and not a part of more recent, unconformable sediments, has been established. The possibility of unconformities within the Allenby Formation has been considered by Rice (1947), Shaw (1952), Russell (1958), and Hills (1962, 1965a). This uncertainty was due to the discrepencies in proposed ages of the sediments based on identifications of megafossils. On the basis of evidence from structure, composition of the sediments, and palynology, however, these same authors considered such a situation unlikely. There are late Tertiary sediments in the basin, however. Mathews and Rouse (1963) made a study of these deposits and found them to be late Miocene or early Pliocene in age, nearly flatlying, and scattered over a wide area in southern

Fig. 3. Stratigraphic relationships of Tertiary deposits
         of the Princeton basin.

Alluvium

Late Tertiary Deposits

←Ashnola Locality

Allenby Formation

←Princeton-Black Coal Seam

Upper Volcanic Formation

Lower Volcanic Formation

Nicola Group (Triassic)

Shale

Coal

Sandstone

Conglomerate

Volcanic Rock

1 cm = 150 meters
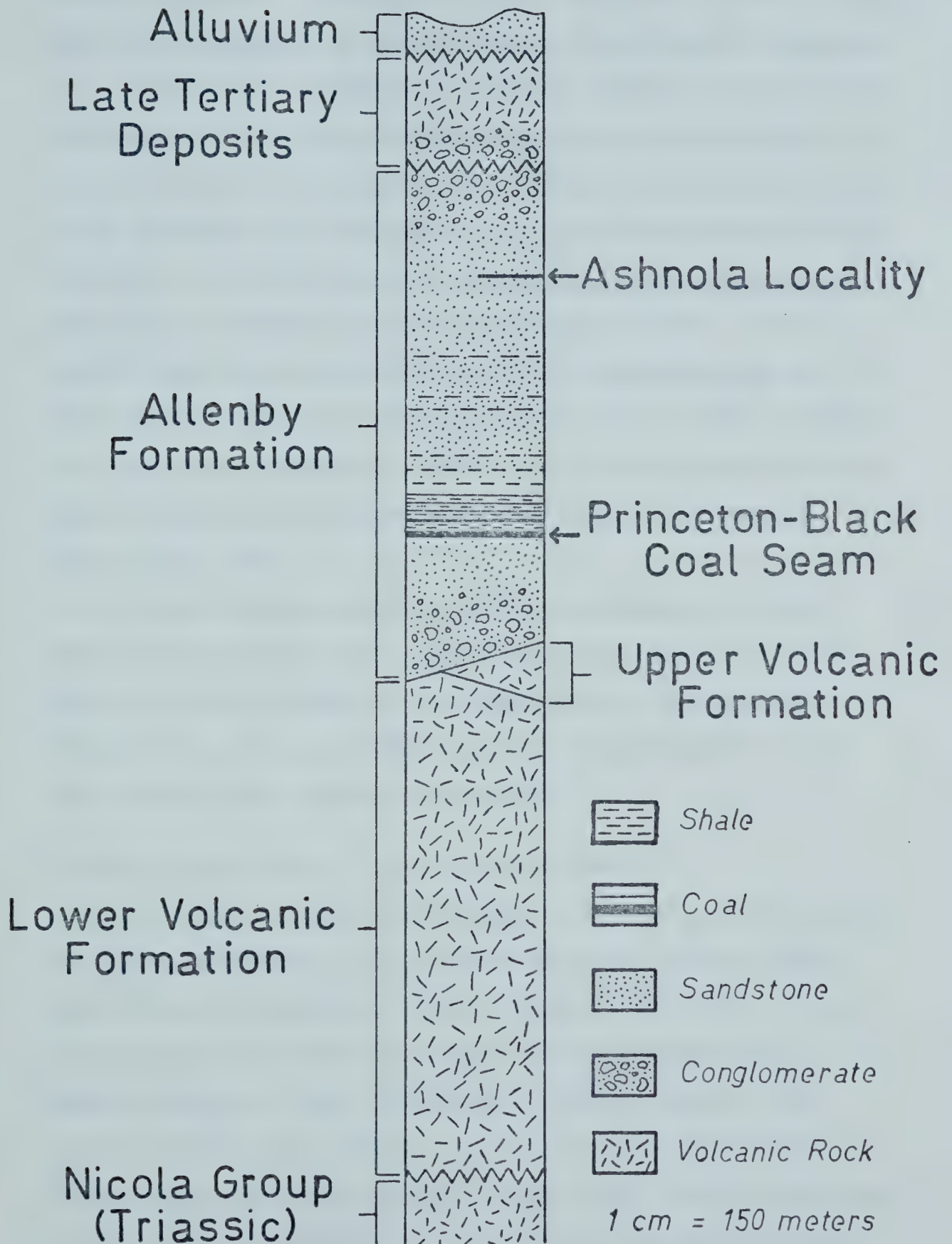
British Columbia. Outcrops of these deposits, however, have not been recognized in the vicinity of the Ashnola locality.

Palynological studies by Boneham (1968) have shown that there was no significant difference between the Ashnola locality and other localities of the Allenby Formation that would indicate an unconformity. Of great importance is the discovery of an abundance of Pistillipollenites macgregorii Rouse at the Ashnola locality by Boneham (1968). This species has been reported from the Allenby Formation by Rouse (1962), Mathews and Rouse (1963), Hills (1962, 1965b), and Hills and Baadsgaard (1967), and is considered to be an index fossil for the Lower and Middle Eocene (Rouse and Srivastava, 1970).

A more detailed account of the stratigraphy of the Princeton basin will serve to clarify the position of the Ashnola locality relative to other beds of the Allenby Formation as well as to the numerous localities that have been sampled for radiometric dating.

Volcanic Formations of the Princeton Basin -

Rice (1947) described Tertiary volcanic deposits above and below sediments in the Princeton basin. Shaw (1952) named these the Upper and Lower Volcanic Formations. The Lower Volcanic Formation outcrops at the southern and western margins of the basin and is there found at its greatest thickness. These volcanics overlay principally the Triassic volcanics of the Nicola Group, and are overlain by the Allenby Formation in the northern and eastern parts

of the basin. The Allenby Formation and the Lower Volcanic
Formation appear to be conformable (Rice, 1947; Shaw, 1952;
Hills, 1962, 1965b). The Lower Volcanics wedge out toward
the north-east and are not found at the northern and eastern
limits of the Tertiary deposits. In this area, however, are
found rocks of the Upper Volcanic Formation. This formation
finds its greatest thickness in the east and apparently
wedges out toward the center of the basin.

Hills (1962) reinvestigated the Princeton volcanics and
found that both Rice (1947) and Shaw (1952) were in error in
placing the Upper Volcanic Formation above the Allenby Forma-
tion. Hills (1962, 1965b) has established that many of the
outcropping volcanics are actually underlying the Allenby
Formation and are possibly a part of the Lower Volcanics.
Hills also refers to a number of smaller volcanic outcrops
that were apparently included in the Upper Volcanic Forma-
tion, but which may be late Tertiary in age. Thus, the
Upper Volcanic Formation of Shaw (1952) does not exist as
such.

Late Tertiary Volcanic Deposits -

Although not directly involving the Ashnola locality,
late Tertiary deposits are found in parts of the basin and
may be responsible to some degree for misinterpretations of
the age of the Allenby Formation (see Discussion). These
once extensive deposits have also shielded the early
Tertiary sediments from severe erosion during the Pleistocene.

Late Tertiary deposits are found in the northern and

eastern parts of the basin and were called the post-Oligocene of Plateau Volcanics by Camsell (1907), but were apparently lumped together with older volcanic rocks to become the Upper Volcanic Formation by Shaw (1952). Hills (1962) recognized late Tertiary deposits when he reviewed the status of the Upper Volcanic Formation, but did not provide a description of them. Mathews and Rouse (1963) found these flat-lying deposits scattered over much of southern British Columbia and believe, as Camsell did, that they represent lavas that once covered the entire area. Three K-Ar dates obtained from these rocks (Mathews and Rouse, 1963) indicate a late Miocene or early Pliocene age.

Camsell (1907) proposed that these once extensive lavas protected the underlying rocks from serious erosion during the Pleistocene Glaciation. They were, however, nearly completely destroyed themselves and now often appear as caps on the tops of the higher hills, where they form outcrops too small to map. The result, after glaciation, is a much greater thickness of the decomposed rocks of the Allenby Formation than would have been possible without such protection.

Mathews and Rouse (1963) also found occasional sedimentary beds within or conformably beneath the volcanic rocks. These authors feel that a number of plant fossils from these beds were collected by early workers and included in a larger collection from the early Tertiary, Allenby Formation. This error may have been responsible, in part,

for the late Tertiary age assignment early workers gave to
the Allenby Formation.

Allenby Formation -

Sediments of the Allenby Formation were first named
and described in detail by Shaw, who states (1952, p.8):

> "The Allenby Formation consists predominantly of
> massive, crossbedded granule- and pebble-conglomerate,
> sandstone, and massive and thinly bedded shale, with
> inter calated beds of coal, carbonaceous siltstone and
> shale, and bentonite. All size gradations between
> conglomerate and siltstone are represented, but
> granule-conglomerate and coarse sandstone seem to
> predominate."

Shaw (1952) noted that the coarser conglomerates were
confined to the lowermost strata, below the major coal
zones, although less coarse conglomerates can be found
throughout the Allenby Formation. These lowermost con-
glomerates were found by Hills (1965a) to contain high
percentages of volcanic detritus of a local origin. Hills
also noted some volcanic flows in this zone.

The composition of sediments was recognized by Rice
(1947) and Shaw (1952) as being primarily granitic in
origin, and Shaw (1952, p. 8) states:

> "The volcanic content has undoubtedly been provided
> by the nearby large areas of the dominantly volcanic
> Nicola group and Cretaceous volcanic rocks that now
> occupy lesser areas."

From a more detailed study of the mineral composition
of the Allenby Formation as well as of the surrounding
volcanics, Hills (1965a) determined the provenance of the
Allenby sediments to be the Osprey Lake Intrusion which
lies to the north of the Princeton deposits and actually

contacts the Allenby Formation on the northern margin.
Hills (1965a) also found evidence for a paleocurrent flow
from the north or northwest.

The existence of unconformities within the sediments
of the Princeton basin was considered unlikely by Rice
(1947), Shaw (1952), Russell (1958), and Hills (1962, 1965a).
However, stratigraphic zonation, based on the nature of the
sediments of the Allenby Formation, was indicated by Shaw
(1952) and Hills (1962, 1965a, b). The lowermost sediments
are primarily conglomerates, and finer grain sediments are
more dominant in the bulk of the upper sediments, although
there is another zone of conglomerates in the uppermost
strata.

Coal has been mined from exposures near the Princeton
townsite since the early part of this century. Although
several seams have been exploited, the Princeton-Black Seam
has been found to be the thickest and most extensive (Rice,
1947; Shaw, 1952). The mapping of this coal seam as well
as the drilling of boreholes in search of coal have proved
very valuable stratigraphically. The Princeton-Black Seam
is the lowest occurrence of mineable coal in the stratigraphic
sequence and has been used by Hills (1962, 1965b) to divide
the Allenby Formation into an upper and a lower unit. The
sediments below the Princeton-Black Seam are over 300 meters
thick and consist basically of coarser conglomerates and
sandstones. Above the Princeton-Black Seam are over 600
meters of basically shaley strata. Hills (1965b) notes that

sandstone lenses increase in frequency and thickness upward
in this upper unit. Since the Princeton-Black Seam is
easily recognized and its extent fairly well known,
localities within the Allenby Formation are often assigned
a stratigraphic position relative to the Princeton-Black
Seam.

The Ashnola locality was found to be about 550 meters
above the Princeton-Black Seam and 850 meters above the
base of the Allenby Formation by Boneham (1968). Although
the locality is near the top of the Allenby Formation, there
are no conglomerates associated with it. A dense, black
shale lies on top of the Ashnola beds, and a sandy shale is
found beneath. Most associated strata have become covered
by slumping, but those that are visible are comprised
basically of sandstone. There is a lack of mineable coal
in the Ashnola area as well as in the northern and eastern
parts of the basin, all of which represent the uppermost
strata of the Allenby Formation. The fact that such an
extensive coal deposit at the Ashnola locality exists in a
zone generally devoid of sizable coal seams would indicate
that the Ashnola locality represents a local phenomenon and
such deposition was not widespread.

Statigraphic zonation has also been recognized within
the Allenby Formation by Hills (1965b) and Boneham (1968)
on the basis of varying abundance of pollen and spore types.
Although species vary in abundance, there are no abrupt
changes in floral composition that would indicate an

unconformity. Hills (1965b) lists a lower Bisaccate Zone (60 meters thick), an _Azolla_ _primaeva_ Zone (250 meters thick), the Princeton-Black Coal Zone (40 meters thick), and a _Pistillipollenites_ _macgregorii_ Zone which can be subdivided into an upper, bisaccate (600 $\pm$ meters thick), and a lower, _Taxodium_ (60 meters thick) dominance subzone. Boneham (1968) basically disagrees with Hills' interpretation, but supports the idea of zonation within the Allenby Formation. It should be noted that Hills based his work on collections made primarily within 60 meters above and 300 meters below the Princeton-Black Seam. Boneham, on the other hand, primarily studied samples taken above the Princeton-Black Coal Zone. The only zone in which both Hills' and Boneham's studies have overlapped is in the _Taxodium_ dominance sub-zone. Of this subzone Boneham states (1968, p. 33):

"Apparently the only stratigraphic zone Hills and I agree upon is his _Taxodium_ dominance subzone."

Boneham goes on to say that he could not substantiate the presence of Hills' lower zones due to the lack of representative sampling. It appears that Hills may have over-interpreted results from his single sample in the upper zone of the Princeton basin and his determination of zonation in the Tulameen (Coalmont) basin. However, consideration of the findings of both Hills and Boneham should give a reasonably accurate appraisal of zonation in the Princeton basin.

The Ashnola locality is well into Hills' _Pistillipol-lenites_ _macgregorii_, bisaccate dominance subzone. Although

Boneham rejects the existence of this subzone on the basis
of a general lack of P. macgregorii and bisaccate grains, P.
macgregorii is exceedingly abundant at the Ashnola locality
(Boneham, 1968) and remains of Pinus form a large component
of the locality's megafossil flora. It is likely that
microecological factors were causing variability which
makes Hills' findings and the flora of the Ashnola locality
apparently incompatable with Boneham's results. The
differences in composition are not sufficient to suggest an
unconformity between the Ashnola locality and other localities
in the basin.

The Ashnola Locality

Age -

    Direct evidence for the age of the Ashnola chert was
presented by Boneham (1968) in the form of Pistillipollenites
macgregorii Rouse, a palynomorph characteristic of the Middle
Eocene (Rouse and Srivastava, 1970). Although no radiometric
dates have been determined for the outcrop, many dates,
indicating a Middle Eocene age, have been recorded for
other deposits within the Allenby Formation as well as for
localities within the Upper and Lower Volcanic Formations
and volcanics from other basins in southern British Columbia
(see Table 1). Since the Ashnola locality has been
established as a part of the Allenby Formation, and there
have been no unconformities found within the Allenby
Formation or between the volcanic and sedimentary deposits

of the basin, these radiometric dates will be considered as representative of the age of the Ashnola chert.

Early workers believed, although frequently with reservation, that the deposits of the Princeton basin, as well as those of other basins in the area, were of late Tertiary age (G.M. Dawson, 1879; J.W. Dawson, 1879, 1890; Scudder, 1879, 1895; Camsell, 1907; Rice, 1947; Shaw, 1952) (See Boneham, 1968).

Evidence for an Eocene age was first presented by Russell (1935) and Gazin (1953) in the form of Tillodont mammal remains, but the fragmentary nature of these fossils did not permit a conclusive age determination.

Both palynological and radiometric evidence became available during the 1960's and established a Middle Eocene age for the Princeton deposits.

Some degree of comparability among the microfloras of the Allenby, Burrard, Kitsilano, McIntosh, Green River, and Fort Union Formations were recorded by Rouse and Mathews (1961), Rouse (1962), and Hills (1965b). Rouse (1962) notes that all except the Fort Union Formation, which is Paleocene, are regarded as Middle Eocene.

Pistillipollenites macgregorii Rouse (1962) , which appears to be characteristic of the Middle Eocene (Rouse and Srivastata, 1970), has been reported from the Allenby Formation by Rouse (1962), Mathews and Rouse (1963), Hills (1962, 1965b), Hills and Baadsgaard (1967), and Boneham (1968). As noted previously, Boneham found this species

in abundance at the Ashnola locality.

Potassium-Argon (K-Ar) dates were recorded by Rouse and Mathews (1961), Mathews (1963), Hills (1965b), and Hills and Baadsgaard (1967). The results of these reports are found in Table 1. Those determinations of Hills and Baadsgaard (1967) were published from Hills' thesis (1965). Where results from the two publications differ, the dates recorded by Hills and Baadsgaard (1967) are used. A few of the samples of Hills (1965b) and Hills and Baadsgaard (1967) have yielded ages which are either far greater or, in one case, much less than the mean. This is attributed to contamination by older rocks in the former, and to the use of glass shards, which do not appear to retain Argon well, in the latter.

The Sunday Creek and Sunday Summit localities are found about 20 miles south of the town of Princeton, and are believed to be in the uppermost part of the Lower Volcanic Formation, or at the base of the Allenby Formation where the sediments are interbedded with volcanics (Rice, 1947; Hills and Baadsgaard, 1967). All localities other than the Sunday Creek, Sunday Summit, Princeton, and Allenby localities, are found in other Tertiary deposits such as those of the Kamloops group (McAbee, Quilchena, Tranquille, Battle Bluff, Savona Mountain), Tulameen or Coalmont basin (Collins Gulch), and Smithers area (Driftwood Creek).

The large number of radiometric dates from a wide range of rock types and localities show excellent agreement

and leave little doubt as to the true age of the Tertiary
deposits. A mean value for the age of the Princeton
deposits is 49 m.y., which places the Allenby Formation
at Middle Eocene.

Correlation of Tertiary Deposits of Southern British Columbia -
The close approximation of the age of the Allenby
Formation with the ages of other Tertiary deposits in
southern British Columbia supports the theories of earlier
investigators such as Camsell (1907), Penhallow (1907), and
Rice (1947) that the Kamloops group and Princeton group are
the same age.

Palynological data is also in agreement with such
correlation. Palynomorphs are generally more readily
available than megafossils and are often more useful in
stratigraphic correlation. Rouse (in Rouse and Mathews,
1961) used both mega- and microfossils and found that the
Princeton, Tranquille and Rock Creek beds were synchronous.
Hills (1965b) apparently was able to find some correlation
among all Tertiary beds that he sampled, from Princeton to
as far north as Smithers.

Although these Tertiary deposits are found in isolated
areas over much of south-central British Columbia and are
of an equal age, it is unlikely that they were at one time
continuous over the entire area. Some of the beds of the
Coldwater and Kamloops groups appear to have been more
extensive at one time, but those of the Princeton basin
were probably never much more extensive than they are at

Table 1. Potassium-Argon dates of Lower Tertiary strata from southern British Columbia. All radiometric analyses were made by H. Baadsgaard, Dept. of Geology, Univ. of Alberta.

[1]R&M - Rouse and Mathews (1961)
 M   - Mathews (1963)(from Hills, 1965b)
 H&B - Hills and Baadsgaard (1967)

Author[1]	Material	Locality	Date (m.y.)
R&M	Biotite	Princeton	48
R&M	Biotite	Tranquille	49
R&M	Biotite	Savona Mountain	45
R&M	Biotite	Rock Creek	49
M	Biotite	Kettle River	48
M	Biotite		46
M	Biotite		53
M	Biotite		48
M	Biotite		
H&B	Andesine	Sunday Summit	50
H&B	Oxyhornblende	Sunday Summit	48
H&B	Oxyhornblende	Sunday Summit	52
H&B	Biotite	McAbee	50
H&B	Andesine	McAbee	48
H&B	Sanidine	Quilchena	79
H&B	Glass Shards	Quilchena	22
H&B	Biotite	Allenby	50
H&B	Andesine	Allenby	49
H&B	Sanidine	Sunday Creek	47
H&B	Sanidine	Sunday Creek	50
H&B	Andesine	McAbee	51
H&B	Biotite	McAbee	57, 56
H&B	Sanidine	McAbee	67, 56
H&B	Oligoclase	Battle Bluff	51
H&B	Sanidine	Battle Bluff	50
H&B	Biotite	Battle Bluff	50
H&B	Biotite	Battle Bluff	48
H&B	Biotite	Collins Gulch	47
H&B	Sanidine	Driftwood Creek	126

the present (Hills, 1965b). The orogenic movements which
initiated deposition in the early Tertiary apparently had
the effect of creating numerous, isolated basins over a
wide area.

Structure -

As noted earlier, the Ashnola locality forms a 10 meter
thick outcrop of interbedded chert and coal that is exposed
on the east bank of the Similkameen River and extends into
the river to form a partial dike. Boneham (1968) determined
the strike to be N 27°E and the dip, 34°N. The beds outcrop
for a short distance up the bank and it was noticed that
they are folded rather sharply some 12 meters above the
water's edge.

Boneham measured each layer of chert and coal (see
Fig. 2) and sampled each for palynological analysis. The
validity of his numbering individual layers is here questioned,
for the thickness of layers is highly variable. Many chert
or coal layers are found to anastomose and the intervening
layer is terminated at that point. There are, however,
several exceptionally thick layers of chert and coal that
were identifiable throughout their entire exposure. With
these layers as markers, it was possible to divide the
outcrop into 9 intervals, each $\frac{1}{2}$-$1\frac{1}{2}$ meters thick, and con-
taining a number of layers of chert and coal. Each of the
9 intervals is separated from others by a broad and con-
tinuous layer of coal. These 9 units are relatively easily
recognizable throughout the outcrop, while numbers applied

to individual layers will vary with position on the outcrop.
I believe that this system of numbering better reflects
intervals of chert formation and gives a more accurate
description of layering of the chert and coal.

Formation -

The outcrop extends into the Similkameen River for
somewhat less than half the stream width and then disappears
into the river bed. On the opposite side of the river is
flat, bottom land which presumably represents former river
channels and flood plain. There is no trace of outcropping
rock on the west bank. The chert beds apparently do not
extend far beneath the river, for Boneham (1968) notes that
there is no trace of chert in the well log of Blakemore
Borehold #1, which was sunk almost directly across the
river from the Ashnola locality. This led Boneham to
believe that the beds were very restricted in lateral
extent and that the bog in which the deposits accumulated
was likewise small in area.

Boneham (1968, p. 37) has reviewed possible theories
for the origin of chert deposits and has lumped them into
two groups:

> "One group claims that the chert is contemporaneously
> deposited with other sediments. The other group
> maintains that chert is a postdepositional replacement
> of the host rock."

An initial inspection of the chert of the Ashnola locality
disposes of the latter group, for there are plant remains
preserved in it and thus could not be a result of post-.

depositional replacement.

A review of similar occurrences of plant-bearing cherts reveals that they have requirements in common for their formation. There must be a source of silicates, which is generally believed to be hot, mineral springs or geysers often associated with volcanic activity. The siliceous waters must be contained in a relatively quiet body of water and be precipitated to form a silica gel covering the bottom of the bog or marsh. Precipitation could be accomplished by excessive evaporation which would create a supersaturated condition (Arnold and Daugherty, 1963), or by a change in pH. Correns (1950) has shown that a change in pH from 9 to 5 will result in the precipitation of 2/3 of dissolved silicates from a concentrated solution. The silicates infiltrate the top layers of debris and mud at the bottom of the marsh and, with time and the expulsion of water, forms chert. Although silicified woods and other resistant plant organs can be found with some frequency in the fossil record, silicified herbaceous forms and more delicate organs are uncommon and almost restricted to beds formed in the above manner.

The rhythmic deposition of chert and coal as found at the Ashnola locality is a very rare occurrence, with the only other known instance being in the Devonian during the formation of the Rhynie chert of Scotland. Kidston and Lang (1917, p. 764) have proposed the following explanation for the formation of the Rhynie beds:

"The whole history of the formation of the Rhynie
Chert zone, at least of that portion from which our
specimens were taken can be clearly read. ... By the
decay of the underground parts of Rhynia and the
falling down of withered stems (for this plant had
no leaves) a bed of peat was gradually formed varying
from an inch to a foot in thickness. The peat was
then flooded and a layer of sand deposited on its
surface. Again the Rhynia covered the surface, and
this process of the formation of beds of peat, with
the deposition of thin layers of sand, went on till
a total thickness of 8 feet had accumulated.

After the formation of 8 feet of alternating peat and
sand local physical conditions must have altered, for
water with silica in solution, possibly discharged
from fumaroles and geysers, poured over the peat bed
and sealed it up."

Of this type of deposition Taliaferro (1933, p. 50)

states:

"The cause of the rhythmic banding of cherts and
shales has been discussed many times and the only
two hypotheses which have survived the test of
critical examination are those of coloidal segregation
and periodic supersaturation."

Boneham (1968, p. 38) elaborates and applies this to

the Ashnola locality:

"Taliaferro goes on to explain what he means by
colloidal segregation. Essentially this can only
happen in sea water since the colloidal particles of
silica must be electrically charged by the dissolved
salts present in sea water before these silica
particles will clump in large enough aggregates to
precipitate. There is no evidence that sea water was
present in the Princeton Basin during Allenby time.
Innundation of the swamp or peat bog by hot water
rich in silicic acid from nearby volcanic sources
seems to be the most likely origin of the silica.
This water was probably hot enough to kill the
vegetation of the bog. As the hot water mixed with
the acidic water of the bog some of the silica pre-
cipitated. When the water cooled, it became super-
saturated with silica and more of it precipitated.
With the gradual cooling of the water, plants were
able to establish themselves and so form another
layer of peat on top of the chert layer. There are
igneous rocks below the tuffs within the Allenby

Formation. Volcanic activity must have been prevalent during Allenby time, so there may have been hot springs in the Princeton Basin."

The cherts of the Eocene, Clarno Formation of Oregon may be comparable to the Ashnola cherts also. Although not found rhythmically interbedded with coal, the Clarno chert appears to represent the soil of an ancient marsh in which permineralization was the result of the precipitation of silicate from mineral-rich hot springs (Arnold and Daugherty, (1963). Arnold and Daugherty (1963, p. 216) proposed that:

"The high evaporation rate coupled with the impeded outflow of the water in the marsh resulted in a build-up of silica in the mucklike soil, leading to development of silica gel. ... Solidification of the mineral-saturated soil and plant parts was the final stage of the process of fossilization which was brought about by the weight of a sheet of lava which finally covered the marsh. This resulted in expulsion of enough water to precipitate and harden the siliceous residue into chert, and at the same time effectively protect the deposit from erosion."

There may be some relationship between the Clarno and Ashnola cherts. Their general appearance is similar, although the Clarno chert has a high ash content which imparts a greyish color. Both localities are roughly the same age and are found in a similar geographical position, and may have been formed as a result of the same uplift and subsidence. It is unlikely that such rare occurrences as these chert beds would occur coincidentally in such close proximity in space as well as time. In addition, an important element in the floras of both the Clarno and Ashnola cherts is Dennstaedtiopsis aerenchymata Arnold and

Daugherty (1964), and it is possible that further research will reveal more similarities in floral composition.

The presence of thick beds of ash below and lava flows above the Clarno chert (Arnold and Daugherty, 1963) indicates a brief development of a flora during a fairly unstable period of volcanism. In this way, the Clarno chert appears most similar to the Deccan Intertrappean Series of India. The Intertrappeans are thin sedimentary layers "trapped" between sheets of lava. It is possible that the Inter-trappeans were formed in much the same way as Arnold and Daugherty (1963) described for the Clarno chert.

Boneham's (1968) conclusions as to the formation of the Ashnola chert layers coincide generally with the observations presented here. The Eocene marsh of the Ashnola locality must have suffered periodic inundation with mineral-rich water. The lignite layers of Ashnola are apparently relatively pure and without silicate, so Arnold and Daugherty's (1963) proposal for a continual influx of minerals and a gradual accumulation of silicates in the muck of the ancient, Clarno marsh is not applicable to the Ashnola locality.

The Ashnola marsh was apparently spring fed and of low kinetic energy, for there are apparently no inorganic sediments in any of the chert or coal layers save one chert layer. This is unlike the Rhynie locality where Kidston and Lang (1917) report quantities of sand being deposited on top of successive layers of peat.

In some of the chert layers at Ashnola there is
preserved a considerable thickness of well-preserved plant
material. This may indicate a rapid accumulation of debris,
a slow rate of decomposition, or both. A slow rate of
decomposition would likely mean acidic conditions in the
marsh and support Boneham's proposal for the precipitation
of a silica gel through the mixing of mineral water with
the water of an acid bog. The rapidity with which per-
mineralization took place is evident in the high degree of
preservation of even the most delicate tissues.

Only the Ashnola and Rhynie localities show rhythmic
bedding of chert and coal, but a floral comparison of the
two is impossible due to the vast difference in age. This
type of formation allows for considerable accumulation of
well-preserved material that contributes to a diversity
unmatched in the Clarno and Intertrappean beds where only
a single layer of chert is found at any one locality. The
various layers of chert record changes in dominance, with
the abundance of some forms varying greatly. This allows
many plants to be studied more thoroughly than otherwise
may have been possible if only one layer were available for
study. It is also possible that seasonal differences
reflected by the included plant parts may be found among
the layers of chert. Such an assumption is supported by
the observation of well developed growth rings in the
twigs and wood fragments of woody dicots and conifers.
As yet, the Ashnola locality has, in the Tertiary, proved

to be unique in the abundance of material, the diversity of the flora, and the quality of preservation. In these respects, it is possible to say that the Ashnola locality is comparable to the best coal-ball localities of the Carboniferous.

Other Chert Beds in the Princeton Area -

The question arises as to the possibility of finding other chert beds in the Princeton basin, or perhaps in neighboring basins, since hot springs such as those believed responsible for the Ashnola chert may have been common in the area. That other chert beds occur in the Allenby Formation was noted by G.M. Dawson in 1879. Having no knowledge of the Ashnola chert, Dawson discovered fossilifer- ous chert at Vermilion Bluff, located on the Tulameen River about 3 miles west of the town of Princeton. The beds of this cliff are of a red to yellow hue which has been imparted by the combustion of a lignite seam, but the siliceous beds have resisted serious metamorphism. Dawson (1879, p. 131B) describes the cliff as follows:

> "On a closer examination of this section, however, it appears that the beds have originally differed in character from those usually found, and it becomes apparent that they have been laid down in the bed of a lake, into which very copious mineral springs have issued. The deposit of the springs has been chiefly siliceous, but there is much calcareous matter, and the water probably also contained iron, and other substances, all of which are now mingled with greater or less quantities or ordinary sediment. ...
>
> The rocks as they now appear consist broadly of sand- stones, shaly argillites and siliceous layers, with some siliceous limestones toward the base of the section, in thin beds. The beds more directly resulting

from the siliceous deposit of the springs are very
varied in character. Black chert-like layers occur,
but generally do not continue far horizontally. Other
beds, similar in texture, are mottled with red, due
to the oxidation of iron, and traversed by tube-like
white or grey markings, which on close inspection
are seen to be silicified grass stems, which have
been included in the mass. One of these materials,
microscopically examined proved to consist of dull
amorphous silica through which cloudy flecks were
scattered, and occasional larger opaque patches,
coloured with iron oxide. The base also held minute
crystals of calcite, irregularly distributed, on
obtuse rhombohedrons, perfectly formed, and almost
resembling cubes. The mass must have been deposited
originally in a gelatinous state, about the stems of
milky chalcedony, turning to crystalline quartz toward
the center of each. The stems have in great part
decayed away before the final consolidation of the
mass, and have collapsed irregularly in the tubes,
though still showing the structure of cellular tissues
and spiral vessels under the microscope. In other
layers, a grey porous material is not uncommon, and
in many cases appears to be almost entirely made up of
silicified vegetable fragments, of which the forms can
scarcely be defined."

The chert of this locality has not been studied in any

subsequent investigation of the Princeton basin, including

the present one. It is my belief that a study of this

chert may prove highly rewarding. Dawson's locality and

the Ashnola locality show that proper conditions for chert

formation were present in the Princeton basin at Allenby

time, and it is quite possible that other localities may

be found.

CHAPTER 3

MATERIALS and METHODS

Materials

Chert blocks were mass collected from the Ashnola
locality in July of 1974 by W.N. Stewart, G.W. Rothwell,
and the author and in August of 1975 by W.N. Stewart, G.W.
Rothwell, R.L. Dennis, and M.S. Brosier. Prior to these
collections, small amounts of material were taken from the
locality by C.A. Arnold and R.F. Boneham in the early 1960's
and by W.N. Stewart, G.W. Rothwell, and M.S. Brosier during
an exploratory trip in May of 1974. Material collected by
Arnold and Boneham was later made available to C.N. Miller
(1973) and C.R. Robison and C.P. Person (1973). All
material from the May, 1974 and July, 1975 collections has
been deposited in the University of Alberta Paleobotanical
Collection. The bulk of the material from the collection
of August, 1975 was taken to Ohio University by G.W. Rothwell,
with a lesser amount brought to the University of Alberta.

The structure and extent of the locality has been
discussed in detail in the previous chapter. The outcrop
consists of approximately 10 meters of interbedded chert
and coal (Fig. 4). Over 30 layers of chert have been
recognized by Boneham (1968), but they have been grouped
into 9 units, numbered from the bottom to the top, in the
present study. For most of the blocks, no attempt was made
to determine and record their precise origin with the outcrop.

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They were pried from the outcrop or picked up at its base
and for about 100 meters downstream where they had been
transported subsequent to weathering free. Collections
were made, however, from each of the 9 units in order to
determine whether or not floral zonation existed within
the outcrop.

Unweathered blocks of chert vary from light grey to
black in color. Weathered faces assume a grey to buff color
with plant material visible on the surface (Fig. 5). It
was suspected, and later confirmed during preparations of
the blocks, that those lightest in color did not contain
much of the original organic residues and had to be thin-
sectioned for study. The opaque, black blocks, on the
other hand, contained considerable organic material and were
easily peeled (see Methods). Another supposition that
proved correct was that these lighter blocks contained
plant parts that were on the whole less well preserved than
did the dark blocks, which is probably due to the greater
length of time required for permineralization as indicated
by the loss of organic matter. For these reasons, efforts
were concentrated on the collection of the darkest chert.
Care was taken, however, to obtain representative samples
of all types of chert.

The texture of the rock was also found useful in the
sorting of material in the field. Rich blocks with good
preservation tended to occur in somewhat irregular shapes
and freshly broken faces were glossy black. Pieces containing

Fig. 4. Closeup of the outcrop showing layers of blocky chert interbedded with coal.

Fig. 5. A block of Ashnola chert with plants evident on the surface (dark, circular markings).

mainly decomposed, peaty material tended to be blocky and freshly broken surfaces had a black, but dull, appearance, giving the impression of a coarser texture.

It was found that the darkest blocks of chert came from the lower levels of the outcrop, while those of the upper layers were quite pale. Most material, then, was chosen from the lower chert layers. In the event that considerable lateral variation may occur within any one layer, chert blocks were retrieved from the greatest horizontal extent accessable.

All layers of chert have been fractured one or more times since deposition. These cracks now contain blue, white, or red siliceous in-fillings. Frequently this fracturing and subsequent cementing has reduced the chert to breccia that contains so disrupted a fossil assemblage as to be useless.

Fortunately the layers of chert have been broken up by recent weathering and blocks of various sizes are easily obtained. Blocks of chert are quite hard and difficult to break and any attempt to do so causes the chert to shatter and thus reduce its value for study.

Since few of the blocks had been exposed and weathered long enough to reveal the plants contained, a large pro-portion of the collection was taken with little idea of what was to be found within. The characters described above are by no means rules, for well-preserved and valuable plants can be found in blocks of a wide range of

color, shape, size, and texture. When mass collecting, however, it is desirable to obtain large quantities of the most productive material, and by following these guidelines, it is possible to return with a minimum of "waste" rock.

Upon initial observation, the plant fragments appear to be preserved in a matrix of silicified mud. However, upon closer examination, it can be seen that this back-ground material is composed of small fragments of wood, leaves, pollen grains, and other organic debris. There is an apparent lack of inorganic detrital material of any kind. Preserved plant organs probably fell directly into this organic debris shortly before or during silicification. The silicates only penetrated the top several inches of debris on the bottom of the ancient marsh and formed a layer of chert which lay on a thickness of peat that would later be compressed to lignite. There appears to have been little or no compaction of the infiltrated layer, for plant parts show almost no evidence of crushing or distortion, and the particles of the organic matrix are quite loosely arranged. The lack of inorganic material indicates an absence of stream flow into the marsh. Thus, plant organs found in the chert represent parts of a plant community that grew adjacent to the depositional area. Some of the rhizomes and roots possess rootlets that ramify through the matrix and have been preserved in situ.

The Clarno chert appears similar to the Ashnola chert in the nature and quality of preservation. As noted

previously, the color of the Clarno chert is grey due to the presence of volcanic ash. The cherts of the Deccan Intertrappean series, however, generally compare less favorably with the Ashnola chert. A large number of the localities yield only small quantities of material showing poorly preserved plant parts, although there is an abundance of material found at Rajahmundry, Sausar, and Mohgaon Kalan. At these three localities there is a great diversity of well-preserved plant parts. However, there is usually not an adequate amount of the original organic material remaining in the specimens from even these rich localities to allow the preparation of acceptable cellulose acetate peels. Thin sections must be made in order to study specimens and serial sections are not easily prepared. Serial photographs, using reflected light, and camera lucida drawings of specimens exposed by progressive grinding, techniques practiced frequently (Chitaley, 1955; Prakash, 1956; Verma, 1956; Paradkar, 1973), cannot provide necessary detail nor stand critical examination. In general, the quality and nature of preservation is comparable to that of the "grey chert" of the Ashnola locality.

All specimens figured in the text are deposited in the paleobotanical collection in the Department of Botony, University of Alberta, Edmonton.

Methods

Blocks of chert are first examined for surface evidence

of embedded plant material. If plant parts are visible, blocks are cut in order that cross sections of axes will most frequently be obtained. If there are no plant organs to be seen, or if those that are seen give no indication of their orientation, then blocks are cut such that the saw kerf is perpendicular to the bedding plane. Blocks are cut into slabs approximately 2 cm. in thickness.

As noted under "Materials", the Ashnola chert is found in a range of color from grey to black. The variation in color is caused by differences in the amount of the original organic residues remaining in the specimens. As a result of these differences, grey and black samples cannot be treated in the same manner.

Specimens in grey blocks, which lack organic residues, must be thin sectioned for study. Thin slices are cut from slabs with a trim saw, fixed to glass slides with thermal plastic, and hand ground until translucent.

Black blocks, however, retain much of their organic material and lend themselves well to study by a modification of the cellulose acetate peel technique of Joy, Willis, and Lacey (1956). Modifications of this technique include etching specimens in full strength, commercial grade (48%) hydrofluoric acid (HF) for 60 to 120 seconds and then neutralizing in a saturated aqueous solution of sodium bicarbonate ($NaHCO_3$). It was desirable to leave the specimens submersed in $NaHCO_3$ for at least 15 minutes in order that most of the HF be removed prior to handling.

Cellulose acetate film of .003 inches thickness was found most suitable, for it resists tearing more so than thinner film, but is itself thin enough to allow critical microscopic examination under oil. Prior to mounting on microscope slides, peels may be demineralized in full strength HF for one minute, neutralized, rinsed, and dried. Peels can be mounted in Harleco Synthetic Resin (HSR) or Permount, and are comparable in quality to the finest ground thin sections.

Bulk maceration with full strength HF was attempted by Miller (1973) in an effort to retrieve pine needles from the matrix, but was found to be completely unsuccessful. The siliceous matrix is apparently all that holds the organic residues together, and the removal of this matrix results in a total loss of structure. This technique, however, is useful in obtaining palynomorphs (Boneham, 1968).

Any attempts thus far to fracture the blocks along the surfaces of leaves or other organs in hopes of finding planes of least resistance have proven unsuccessful. Blocks fracture along ancient fracture lines that are now in-filled with silicates, or fracture conchoidally, showing no respect for the plant parts contained.

CHAPTER 4

SYSTEMATICS

Class: Filicopsida

Order: Filicales

Family: Polypodiaceae

Sub-family: Dennstaedtioideae

Dennstaedtiopsis aerenchymata Arnold and Daugherty (Figs. 6-18)

DESCRIPTION - Rhizomes and petioles of this polypodiaceous
fern are common in the chert, occasionally being the dominant
form of vegetation present, but usually found as a minor
component in association with other types of plants.
Identification was based on comparisons with material
described by Arnold and Daugherty (1964), which is the
only other report of this species.

The solenostelic rhizomes (Fig. 7) are cylindrical,
5-12 mm in diameter, possess aerenchymatous tissue in both
the pith and cortex, and are covered with multicellular
hairs (Fig. 8). Petioles (Fig. 9) are naked, possess
aerenchyma, and arise singly and at widely spaced intervals.
Each petiole has a single trace, which Arnold and Daugherty
described as having "... the shape of an inverted bowl with
bulbous base and flared rim." Plantlets are often associ-
ated with the production of petioles (Figs. 12-17).

Xylem elements are mostly scalariform, but spirally
thickened elements were reported in protoxylem cells by
Arnold and Daugherty (1964). Xylem maturation is exarch

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with several clusters of protoxylem cells found around the metaxylem. From these protoxylem points arise the root traces (Fig. 7). To both the interior and exterior of the xylem are identical series of tissue zones (Fig. 18). Immediately adjacent to the xylem is a phloem zone. A single layer of cells of the pericycle separates the phloem from the endodermis and is distinguishable from the former by the darker contents of the cells and from the latter by the vast difference in size. The cells of the endodermis are minute and often not recognizable. A layer of weakly developed sclerenchyma just a few cells thick separates the endodermis from the aerenchyma. The aerenchyma is composed of radially elongate air spaces separated by uniseriate partitions. Interior to the inner aerenchyma is a solid pith of vertically elongate cells. Next to the outer aerenchyma is a thin band of solid, parenchymatous cortex followed by a very weakly developed outer layer of sclerenchyma. A soft, outer cortex only a few cells thick lies exterior to this and is covered by an epidermis bearing simple, multicellular hairs of a variable density.

DISCUSSION - The identification of Dennstaedtiopsis aerenchymata by Arnold and Daugherty (1964) was based solely on vegetative features, so a definite affinity with the extant genus Dennstaedtia could not be determined. As in the Clarno material, no sporangia or well-preserved laminae were found, although laminae without recognizable structure are occasionally found attached to midribs (Fig. 11).

Higher portions of the fronds must have undergone decay
prior to infiltration. However, Arnold and Daugherty found
that marked vegetative similarities exist between the fossil
and Dennstaedtia and state (1964, p. 68):

> "The accumulated evidence, incomplete though it is,
> does seem, however, to point quite convincingly to a
> place in the subfamily Dennstaedtioideae of the
> Polypodiaceae. Relationship with any particular
> genus is less certain, though there are unmistakable
> resemblances with certain species of Dennstaedtia."

The most apparent difference between the fossil and
Dennstaedtia is an adaptation to an aquatic habitat
(aerenchyma) exhibited by the former that is unknown in
living Dennstaedtia. However, Kaplan (1970) has found
that leaf anatomy may vary greatly even among populations
of a single species. This difference, then, may be of
minor significance.

<div align="center">

Order: Filicales

Incertae sedis

Fern A (Figs. 22-25)

</div>

DESCRIPTION - Petioles of this fern are ovoid, with an
adaxial groove. A sclerenchymatous hypodermis surrounds
a solid cortex. The stele is comprised of two hippocampus-
shaped traces and is referred to as the Onoclea-type of
stelar configuration by Ogura (1972) (Figs. 20-25). The
traces fuse at more distal levels (Fig. 25). No rhizomes
or laminate pinnules have been found.

DISCUSSION - Ogura (1972) has found that the _Onoclea_-type of stelar configuration occurs in the Aspidiaceae (_Matteuccia_, _Athyrium_, _Diplazium_, _Onoclea_, _Woodsia_, _Peranema_, _Hypodematium_, _Cystopteris_, etc.) and in a few species of the Pteridaceae (_Onychium_, _Pteris_, _Adiantum_).

The most distal portions of these petioles, where the traces have fused, appear very similar to the smallest petioles of _Dennstaedtiopsis aerenchymata_. This is especially true where the preservation is poor, but under conditions of good preservation they are distinguishable by such characters as the greater degree of endodermal wall thickening in the unidentified fern. This fern is not common in the chert and does not appear to be associated with _Dennstaedtiopsis_.

Fern B (Figs. 19-21)

DESCRIPTION - Both large petioles and rhizomes of this fern are represented, but none of the more distal portions of the fronds have been found. Preservation of the rhizome is poor and has not permitted an accurate description beyond identifying it as a dictyostele (Fig. 19). Petioles, on the other hand, are well-preserved and clearly show an outer, sclerenchymatous layer surrounding a primarily aerenchymatous cortex (Figs. 20 and 21). The stele is composed of several bundles, each surrounded by its own endodermis. These bundles are assembled in a bowl-shaped

Fig. 6. <u>Dennstaedtiopsis</u> <u>aerenchymata</u>. Cross sections of
several rhizomes and petioles showing variability
in the size of rhizomes and the difference in size
between proximal and distal portions of the petioles.
P1094 B bot X 4.3.

Figs. 7 - 11. *Dennstaedtiopsis aerenchymata.* (h =
               hairs; l = lamina; m = midrib; r = root;
               rt = root trace.)

   Fig. 7. Cross section of a rhizome showing general
            features. Note root traces and departing
            roots. P1194 F bot X 8.

   Fig. 8. Cross section of rhizome showing cortex
            and epidermis. Note multicellular epidermal
            hairs. P1194 C top X 22.

   Fig. 9. Cross section of large petiole showing gen-
            eral features. Note the recurved, adaxial
            arms of the vascular strand. P1194 C top X 13.

   Fig. 10. Midrib attached to the distal portion of a
             petiole. P1233 C bot X 34.

   Fig. 11. Midrib with attached lamina. This illus-
             trates the poor quality of preservation in
   this portion of the frond. P1247 E bot X 34.

Figs. 12 - 17.   *Dennstaedtiopsis* *aerenchymata*. Serial sections of a rhizome showing the production of a leaf and a plantlet. Fig. 17 has been taken from a second specimen due to decreasing quality of preservation in a similar portion of the rhizome used for Figs. 12 - 16.

Fig. 12.   Cross section of the rhizome showing the still intact vascular cylinder. Note the expansion of vascular tissue on the upper side of the stele. Pl233 A21 X 6.

Fig. 13.   The vascular cylinder has opened in the region where the enlargement occurred. The trace is departing to the left. Pl223 A6 X 6.

Fig. 14.   As the gap in the vascular cylinder widens, a plantlet trace begins to form as a bulge in the developing leaf trace. This and the following two figures were taken from opposite sides of the saw kerf to Figs. 12 and 13. For this reason Figs. 12 and 13 appear as mirror images to Figs. 14 - 16. Pl223 B1 X 6.

Fig. 15.   The stele of the plantlet is nearly free from the parent rhizome. Note root production by the plantlet. Pl223 B7 X 6.

Fig. 16.   The plantlet is now departing, but the quality of preservation is deteriorating. Serial sectioning of this specimen was discontinued. Pl223 B21 X 6.

Fig. 17.   The series is continued by a second specimen showing leaf trace departure. The vascular cylinder of the rhizome is now closed. Pl194 G top X 6.

Fig. 18.   *Dennstaedtiopsis* *aerenchymata*. Cross section of the vascular cylinder of a rhizome. (a = aerenchyma, e = endodermis, pc = pericycle, ph = phloem, scl = sclerenchyma, x = xylem). Pl204 K bot X 58.
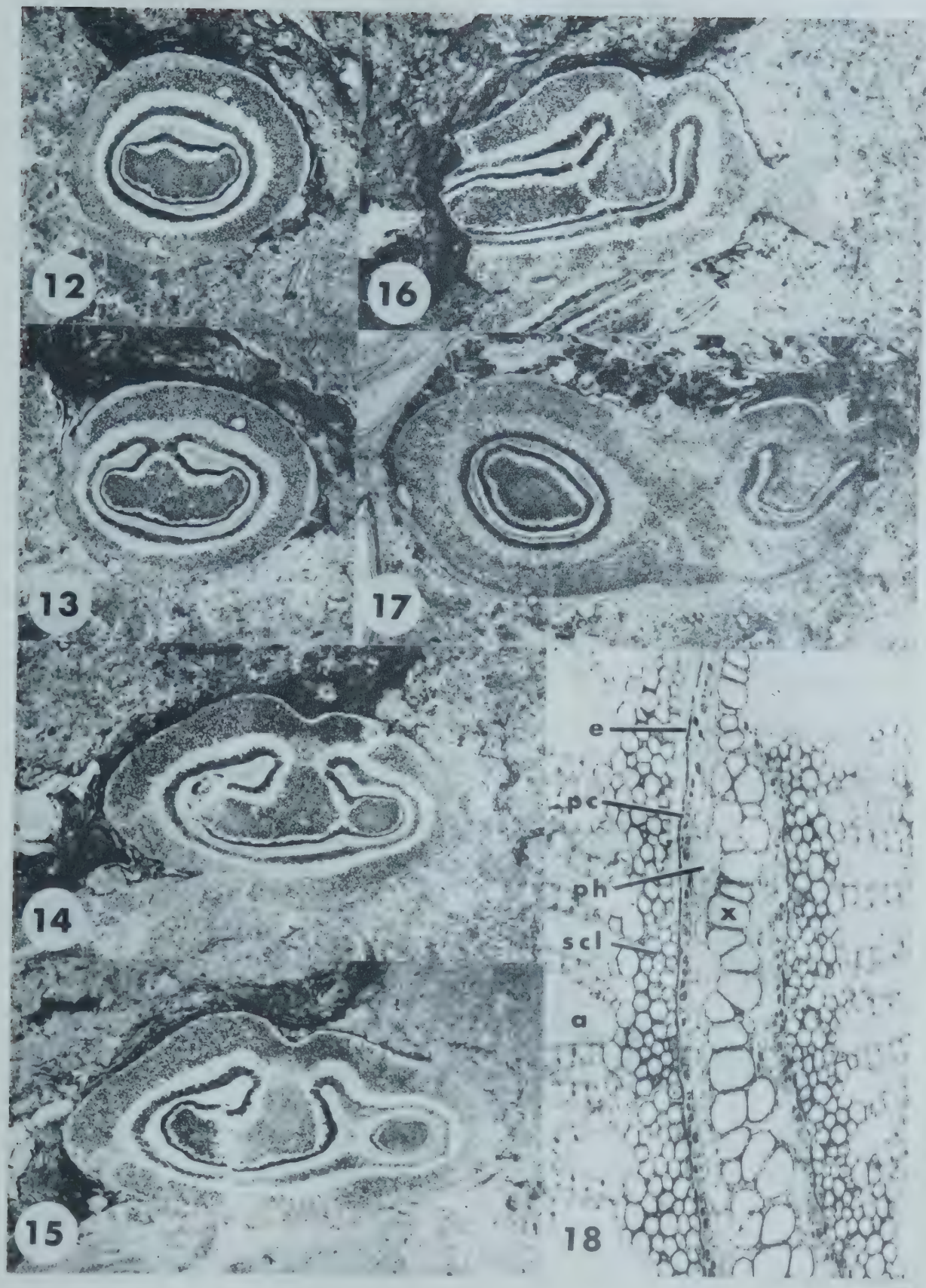
configuration. The two bundles forming the mouth of the bowl (adaxial traces) are considerably larger than the others and possess a recurved, adaxial arm. Other traces are bar- or C-shaped. This type of stelar configuration is known as the Aspidium-type (Ogura, 1972).

DISCUSSION - The Aspidium-type of stelar configuration is found in the Aspidiaceae (Dryopteris, Polystichum, Aspidium, Acrophorus, Elaphoglossum, Bolbitis, Egenolfia, etc.) and the Blechnaceae (Blechnum, Doodia, Brainea, Woodwardia, etc.) (Ogura, 1972). Rhizomes with dictyosteles of various types are common in both families.

Ogura (1972) has proposed that the Onoclea-type of stele gave rise to the Aspidium-type by a proliferation of traces. In fact, the most distal portions of the latter type, where the smaller, medial traces have fused to the larger, adaxial ones, actually appear to have the Onoclea-type of configuration. It is possible, then, that Fern A, which is only represented by small petioles, may be the distal portions of petioles of Fern B. As yet, there is little evidence to support or negate this primarily due to the infrequency with which these forms are found. They have not yet been found associated with one another, and aerenchyma has not been seen in Fern A, so they are here treated as separate entities.

Class: Coniferopsida
Order: Coniferales
Family: Pinaceae
Pinus (Figs. 26-53)

Remains of Pinus can be found in nearly every chert layer and have been the subject of a detailed study by Miller (1973). Miller proposed the names Pinus arnoldii and P. similkameenensis for reproductive and vegetative remains respectively. Although there is only one type of each organ present, Miller found that vegetative and reproductive organs appeared to represent different subgenera of the genus Pinus and was reluctant to place them in the same species.

Pinus arnoldii

DESCRIPTION - This species is based on seed cones that measure 5 - 6 cm in length and 2 - 2.5 cm in diameter. The wood of the vascular cylinder has an abundance of resin canals and an indistinct growth ring. The cortex is comprised of three layers: an inner, parenchymatous layer of small cells; a middle cortex of large parenchyma cells and resin canals; and an outer layer of sclerotic cells (Fig. 27).

Bract and scale traces arise as a complex which divides into the respective traces in the outer cortex

Figs. 19 - 21.   Order Filicales, Incertae sedis (Fern B).

Fig. 19.   Cross section of a rhizome producing leaves.
Two petiolar steles are seen in the right
and left regions of the rhizome while a pe-
tiole has recently departed above.   Note
that aerenchyma is not apparent in the most
proximal portions of the petiole, but well
developed aerenchyma is found in more distal
regions.   Pl247 C top X 5.

Fig. 20.   Cross section of a petiole showing well
developed aerenchyma and a dissected stele.
Note the recurved arms of the two adaxial
bundles.   Pl247 B bot X 15.

Fig. 21.   Cross section of a petiole showing fusion
of a small, median vascular bundle to an
adaxial bundle.   Pl247 D top X 15.

Figs. 22 - 25.   Order Filicales, Incertae sedis (Fern A).

Fig. 22.   Cross section of a petiole showing general
features.   Note the two hippocampus - sha-
ped traces and the absence of aerenchyma.
Pl179 D top X 28.

Fig. 23.   Cross section of a small petiole.   P 1182
I bot X 39.

Fig. 24.   Cross section of a very small petiole which
is still supplied by two vascular traces.
Pl182 I bot X 63.

Fig. 25.   Cross section of a very small petiole show-
ing fusion of the abaxial margins of the
traces.   Pl182 J top X 70.

of the cone axis. The bract trace retains its terete shape as it diverges from the compound trace and passes into the trace. The scale trace, however, loses its circular outline and becomes flattened upon entering the scale and eventually divides into 10 to 15 traces.

The bracts are 4 - 5 mm long and are free of the scale for its entire length (Fig. 28). The ovuliferous scales are 16 - 20 mm long and 4.5 - 6.0 mm wide and have 2 adaxial seed cavities near the base and an inflated apex with an apophysis and an umbo (Fig. 28).

Seeds have been discovered both in cones (Fig. 30,32), and in a dispersed state (Fig. 31). A wing (Fig. 32) is present before dispersal, but has not been found on isolated seeds.

DISCUSSION - That the cones are attributable to the genus Pinus was determined by Miller (1973) on the basis of the presence of an inflated apex and umbo and the restriction of resin canals of the scale base to the abaxial side of the vascular tissue.

Miller had more difficulty in relating Pinus arnoldii with an extant subgenus or section. The inflated scale apex and dorsal umbo are suggestive of the subgenus Pinus, although a few species of the section Parrya, subgenus Strobus, have similar features. Internal structure including the nature of the outer cortex is similar to the subsections Contortae, Oocarpae, and Sylvestres of the section Pinus, subgenus Pinus. However, most species of the Contortae

and Oocarpae produce serotinous, asymmetrical cones and
P. arnoldii appears to have had neither feature. Miller
chose species of the subsection Sylvestres as those to
which P. arnoldii showed most similarity.

Miller notes, however, that P. arnoldii does show
external similarity to certain species of the section
Parrya of the subgenus Strobus. In both cases cones are
long and cylindrical and scales have an inflated apex and
dorsal umbo. Miller doubts a close relationship between
P. arnoldii and species of the section Parrya since P.
arnoldii has small seeds, large pith cells, a small gap
left by the departure of the bract-scale trace complex,
and the branching of this complex in the outer cortex
rather than the inner cortex as in the extant species.

Miller, then assigned P. arnoldii to the subsection
Sylvestres, section Pinus, subgenus Pinus, but acknowledged
the possibility of other affinities.

Pinus similkameenensis

DESCRIPTION - Small and large stems, short shoots and
needles, and roots assignable to this species are abundant
in the chert and are invariably present when cones of P.
arnoldii are found.

Needles and Short Shoots - Needles are approximately 0.5 mm
wide, have a single vascular trace, and are borne in fascicles
of five (Figs. 46, 48). Miller determined their length to be

at least 2.3 cm, but could find no intact leaves, so their actual length was probably much greater (possibly several times that length).

The vascular bundle is surrounded by transfusion tissue. External to this is a prominant endodermis. Mesophyll is composed of very irregularly shaped cells with dentate walls. Beneath the epidermis is a 1 - 2 cell thick layer of hypodermal fibers. Two resin canals are found on the dorsal side of the leaf and are usually external. Stomata are absent from the dorsal surface, but are present in rows on both ventral surfaces (Miller, 1973).

Dwarf shoots are 1.0 - 1.5 mm in diameter and about 2.0 mm long. Miller could find no needle clusters with intact fascicle sheaths and presumed that they were deciduous as they are in modern species of the subgenus Strobus. Some fascicles retaining their sheaths have been found in the present study (Figs. 45, 46). The immaturity of the needles attached to these fascicles lends support to Miller's premise that the sheaths were deciduous.

Wood - Both vertical and horizontal resin canals are present and both are surrounded by thin-walled epithelial cells (Figs. 35, 37). Rays are uniseriate and 1 - 8 cells tall or, where a resin canal is involved, biseriate and 10 - 16 cells tall (Fig. 38). Tracheids have uni- or biseriate circular bordered pits on the radial walls (Fig. 39) and smaller, scattered circular bordered pits on

the radial walls (Fig. 39) and smaller, scattered circular
bordered pits on the tangential walls (Fig. 38). In the
cross-field, ray parenchyma cells were found by Miller to
possess 1 - 4 circular, simple pits (Fig. 40). In the
present study I have also found fenestriform pitting in
the cross-field (Fig. 41). Ray tracheids (Fig. 42) are
present but not common. They have smooth walls and small
circular bordered pits.

The cortex has been preserved in a number of the
smaller stems and it is possible to recognize phloem and
cork zones. Miller has followed dwarf shoot traces through
the cortex to the bases of dwarf shoots. Although there
have been no dwarf shoots found attached to the twigs,
evidence presented by Miller is strongly suggestive of
their former connection.

Roots - Pinaceous roots are often found in association
with remains of P. arnoldii and P. similkameenensis
(Figs. 43, 44). These roots are di-, tri-, and tetrarch
and range in size from 3 mm to 3 cm in diameter. Wood and
cortex is frequently very well preserved. Resin canals
(Fig. 44) are abundant and are lined with thin-walled
epithelial cells. Many roots possess lateral roots still
in attachment (Fig. 43) and have been preserved in situ.

The presence of resin canals with thin-walled epithelial
cells allows these roots to be referred to the genus Pinus.
On the basis of association with remains of P. similkameen-
ensis and of there being no other types of pinaceous remains

present, these roots are assigned to P. similkameenensis

(since the position of P. arnoldii is presently in question

and all other pinaceous vegetative remains have been referred

to P. similkameenensis, it is best to assign the roots to

P. similkameenensis).

DISCUSSION - It appears that all vegetative organs belong

to a single species. Some of the wood that I have examined

appears to differ from that which Miller examined in that

cross-field pitting is fenestriform rather than being

composed of smaller, circular pits. However, there is as

yet no other evidence for there being two types of wood

present and I suspect that this difference reflects natural

variability in the wood of P. similkameenensis. The dis-

covery of fenestriform pits does alter the interpretation

of the wood proposed by Miller (1973).

Both needles and wood were identified as belonging to

the subgenus Strobus. Miller found the needles to be

anatomically inseparable from those of certain living

species of the section Strobus (Pinus monticola, P.

parviflora, P. puece, P. strobiformis, and P. strobus).

Harlow (1931) described the needles of these species as

having a generalized structure from which other quinate

needle types have evolved. The presence of such a needle

type in P. similkameenensis of Eocene age lends support

to Harlow's (1931) theory.

The fossil wood was referred to the subgenus Strobus

(Miller, 1973) on the basis of smooth-walled ray tracheids and of pitting on the tangential walls of the tracheids. The only point of dissimilarity is the much greater number of ray tracheids found in the modern species. Within the subgenus Strobus, Miller identified the wood as belonging to the section Parrya. He found the major difference between members of the section Strobus and the fossil to be the lack of fenestriform pits in the cross-field of the latter.

These findings led Miller to describe the vegetative remains of P. similkameenensis as having a combination of features of both sections Strobus and Parrya of the subgenus Strobus. With the discovery of fenestriform pits in P. similkameenensis, a much closer relationship to the section Strobus is established. Variability in the cross-field pitting in P. similkameenensis may prove to be normal in modern species upon further investigation of extant pine, or it may indicate that, vegetatively, P. similkameenensis and perhaps the section Strobus were less well defined in the Eocene.

Relationships between Pinus arnoldii and P. similkameenensis - Since Miller (1973) could find only one type of each organ present in his samples, he believed that they may all belong to a single species. Miller states that (1973, p. 117):

> "Such a species would thus have features that are generally regarded as distinctive of the two main subdivisions of the genus, and this mixing of characters would further imply that the subgenera Pinus and Strobus may not have existed as separate lines of specialization in the Eocene."

However, Miller could not place the organs into one species because an organic connection is lacking and he was not able to make an extensive survey of the Ashnola locality to determine if other types of organs were to be found elsewhere in the outcrop. If two species of Pinus were in the vicinity, two types of at least one organ would be expected to occur in the chert. As yet I have found no organic connection, but there is still only one type of each organ known. This is strong evidence for combining P. arnoldii and P. similkameenensis into a single species. Furtheremore, Miller did notice a resemblance between P. arnoldii and certain species of the subgenus Strobus. Although evidence for a single species is gaining, I believe it is not possible yet to unite P. arnoldii and P. similkameenensis. Further speculation about the relationships between the subgenera Pinus and Strobus should await proof that P. arnoldii and P. similkameenensis are the same species.

Pinus sp.

DESCRIPTION - Pinaceous pollen cones occasionally occur in association with remains of Pinus arnoldii and P. similkameenensis. The cones are ovoid and about 5 mm in length and 3 mm in diameter (Figs. 49, 50). Each micro-sporophyll bears two abaxial pollen sacs that are usually empty, but some still contain pollen (Fig. 51). Pollen

grains are bisaccate and of the Finus-type (Figs. 52, 53).
Preservation does not appear to be good enough to allow an
anatomical study of the cone axis and microsporophylls.

DISCUSSION - That these cones belong to the genus Pinus is
indicated by the type of pollen grains present. However,
identification within the genus must await detailed study.

Attachment of these cones to associated twigs of P.
similkameenensis has not yet been found but the close
association of these remains and the absence of other types
of pinaceous remains in the chert strongly suggests the
possibility. If they are found to belong to P. similka-
meenensis, these pollen cones may provide an insight into
the relationships between P. arnoldii and P. similkameenensis.
The possibility that all these organs may represent one
species is important, for it would represent one of the
most completely known species of fossil conifers.

Family: Taxodiaceae
Metasequoia sp. (Figs. 54-73)

Taxodiaceous remains are frequent in the chert and
occur as wood fragments, twigs, leaves, and pollen cones.
While only one type of each organ is present, the different
organs show a combination of features found in two modern
genera. Both pollen cones and wood show affinities to
extant Metasequoia, but the leaves are anatomically most

similar to <u>Taxodium</u>.

Pollen Cones

DESCRIPTION - Taxodiaceous male cones are numerous and have been studied in some detail by Rothwell (1975) , and much of the following description has been adopted from his work. The cones are 3.1 - 5.0 mm in length and 1.8 - 3.0 mm in diameter and bear numerous, spirally arranged sporophylls subtended by imbricate, scale-like leaves. Subsequent to the publication of the above-mentioned abstract, Rothwell (personal communication) found that the subtending leaves were decussately arranged and that this pattern did not persist in the sporophylls. Each microsporophyll bears three sporangia filled with spheroid, papillate pollen (Fig. 57). Pollen grains are from 23 to 28 um in diameter. Although microsporophylls are generally not well preserved and cellular detail has not been available, a single, large mucilage duct is clearly evident in each (Fig. 55).

DISCUSSION - Initially Rothwell (1975) believed that the fossil cones were comparable to <u>Metasequoia</u>, <u>Sequoia</u>, and <u>Sequoiadendron</u>. He has since determined that features of scale-leaf arrangement, nature of microsporophylls, and the number of microsporangia per microsporophyll make the fossil cones almost identical to cones of <u>Metasequoia</u> <u>glyptostroboides</u>.

Figs. 26 - 28. *Pinus arnoldii*. (b = bract, rc = resin
               canal, sa = scale apex, sb = spine base,
               sc = seed cavity, tc = scale trace complex).

Fig. 26. Cross section at approximately the middle
          of the cone showing general features.
          P1040 C top X 4.5.

Fig. 27. Closeup of the cone axis of the specimen
          illustrated in Fig. 26. Note the departure
          of two scale trace complexes to the left.
          P1040 C top X 10.

Fig. 28. Longitudinal section through bracts and
          scales of f cone showing the inflated scale
          apex and dorsal umbo. Note the former point
          of attachment of a spine. The object pro-
          jecting from this point into the matrix may
          be the spine, but attachment has not been
          demonstrated. P1143 A X 9.

26

27

28

tc

rc

tc

sb

sa

b

sc
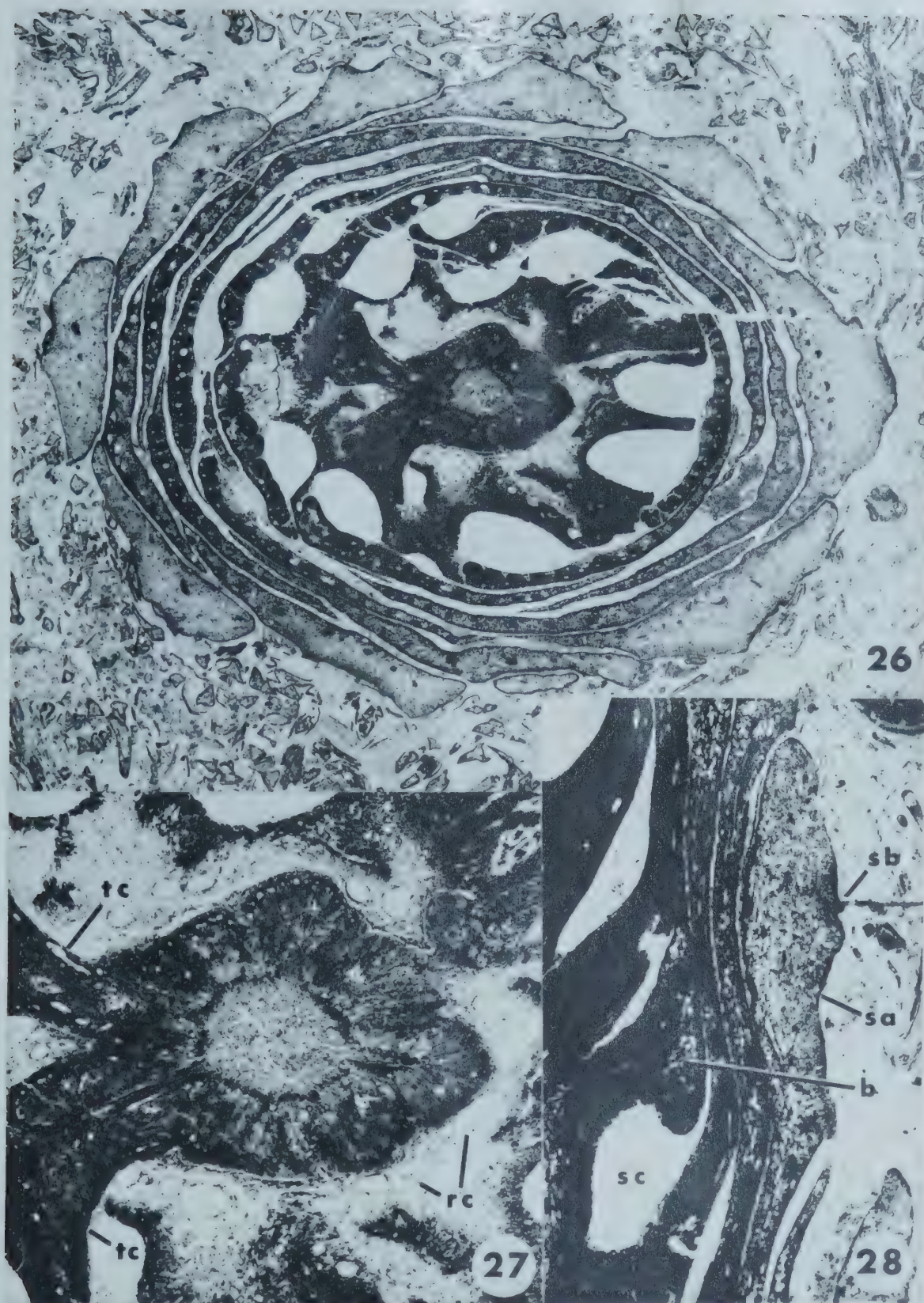
Figs. 29 - 32. *Pinus arnoldii*. (b = bract, s = scale,
                sc = seed cavity, w = wing.)

    Fig. 29.   Oblique longitudinal section of a cone
                showing general features. Pl143 A X 3.

    Fig. 30.   Cross section of a cone with a seed. Pl210
                I Bot X 3.6.

    Fig. 31.   Seed in a dispersed state. No wing was
                found attached to this seed. Pl143 E bot
                X 26.

    Fig. 32.   Closeup of the seed shown in Fig. 30.
                Note the attached wing. Pl210 I bot X 15.
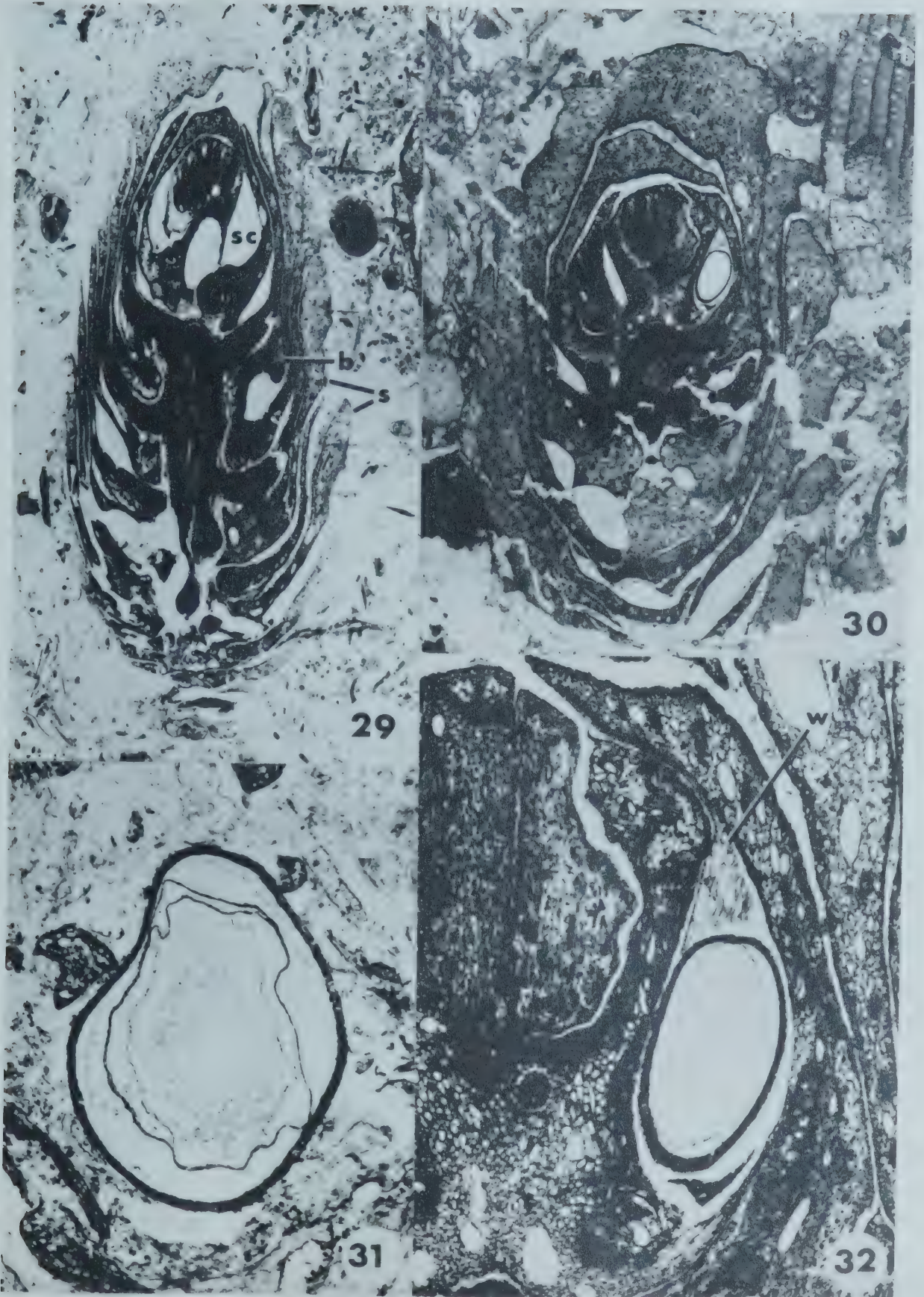
Figs. 33 - 36.   *Pinus similkameenensis*. (sss = short shoot
                 scar, sst = short shoot trace.)

    Fig. 33.   Cross section of a large, decorticated axis.
               P1193 A X 2.4.

    Fig. 34.   Pith region of the stem shown in Fig. 33.
               P1193 A X 42.

    Fig. 35.   Portion of secondary wood showing the dis-
               tribution of resin canals. Note the thin-
               walled epithelial cells lining the resin
               canals. P1193 A X 23.

    Fig. 36.   Cross section of a twig. Note the departure
               of a short shoot trace on the lower right
               and the scar left by the abscission of a
               short shoot on the left. P1210 G bot X 15.

33

34

35

sss

sst

36
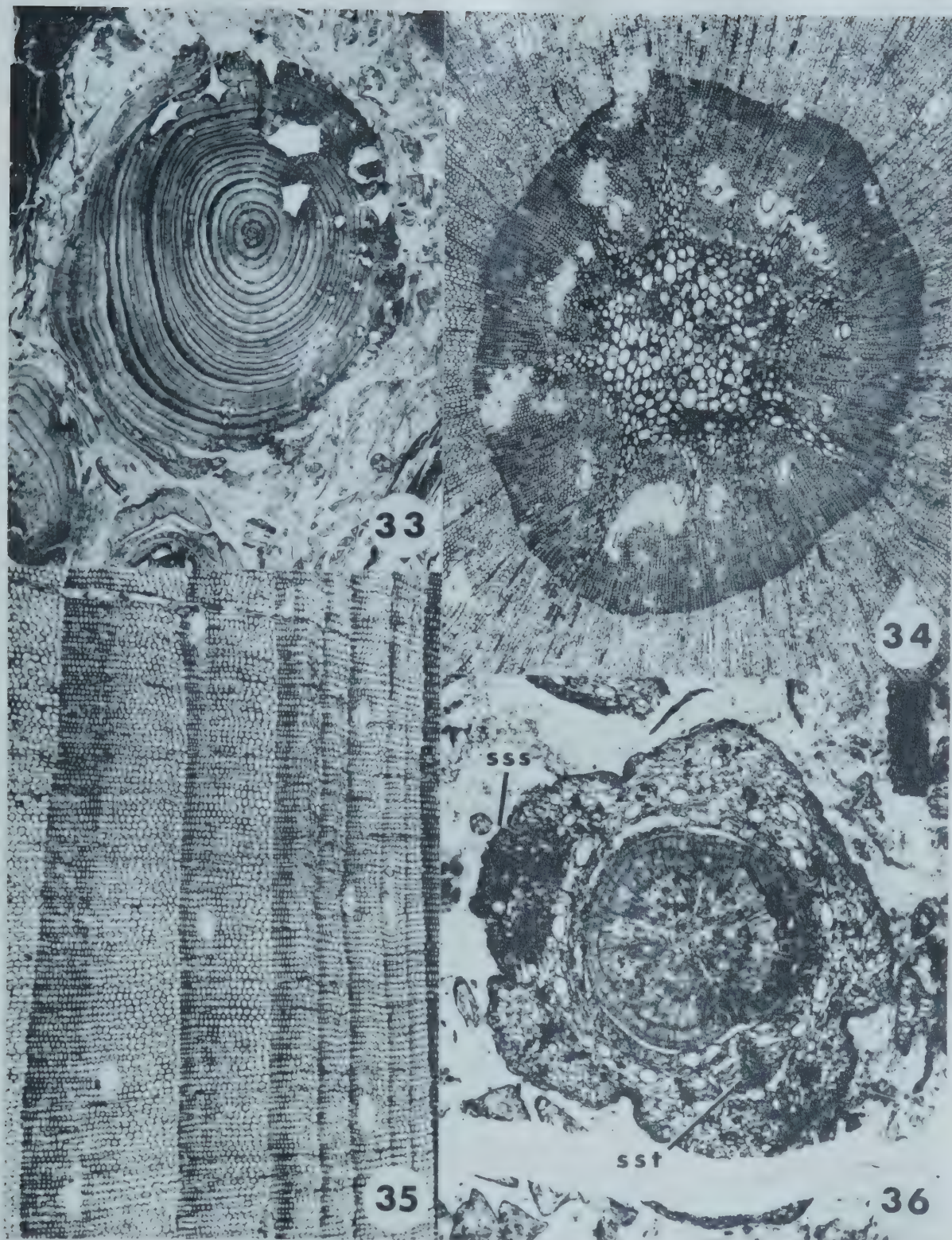
Figs. 37 - 42. *Pinus similkameenensis*. Tangential and
                radial sections of wood. (hrc = horizontal
                resin canal, tp = tangential pit, vrc =
                vertical resin canal).

    Fig. 37. Tangential section showing heterogeneous
              ray structure. Pll01 I X 38.

    Fig. 38. Enlarged portion (tangential) of Fig. 37.
              Note the thin-walled epithelial cells
              lining the horizontal resin canals. Note
              also the pitting on the tangential walls
              of the tracheids. Pll01 I X 138.

    Fig. 39. Radial section showing general features.
              Pll01 I X 38.

    Fig. 40. Radial section showing cross-field pitting.
              The small, circular pits of this specimen
              closely resemble the pits figured by Miller
              (1973). Pll43 E top22 X 235.

    Fig. 41. Radial section showing cross-field pitting.
              Note the large, fenestriform pits exhibited
              by this specimen. Pll01 I X 340.

    Fig. 42. Radial section showing ray tracheids on the
              margins of a ray. Pll01 I X 320.
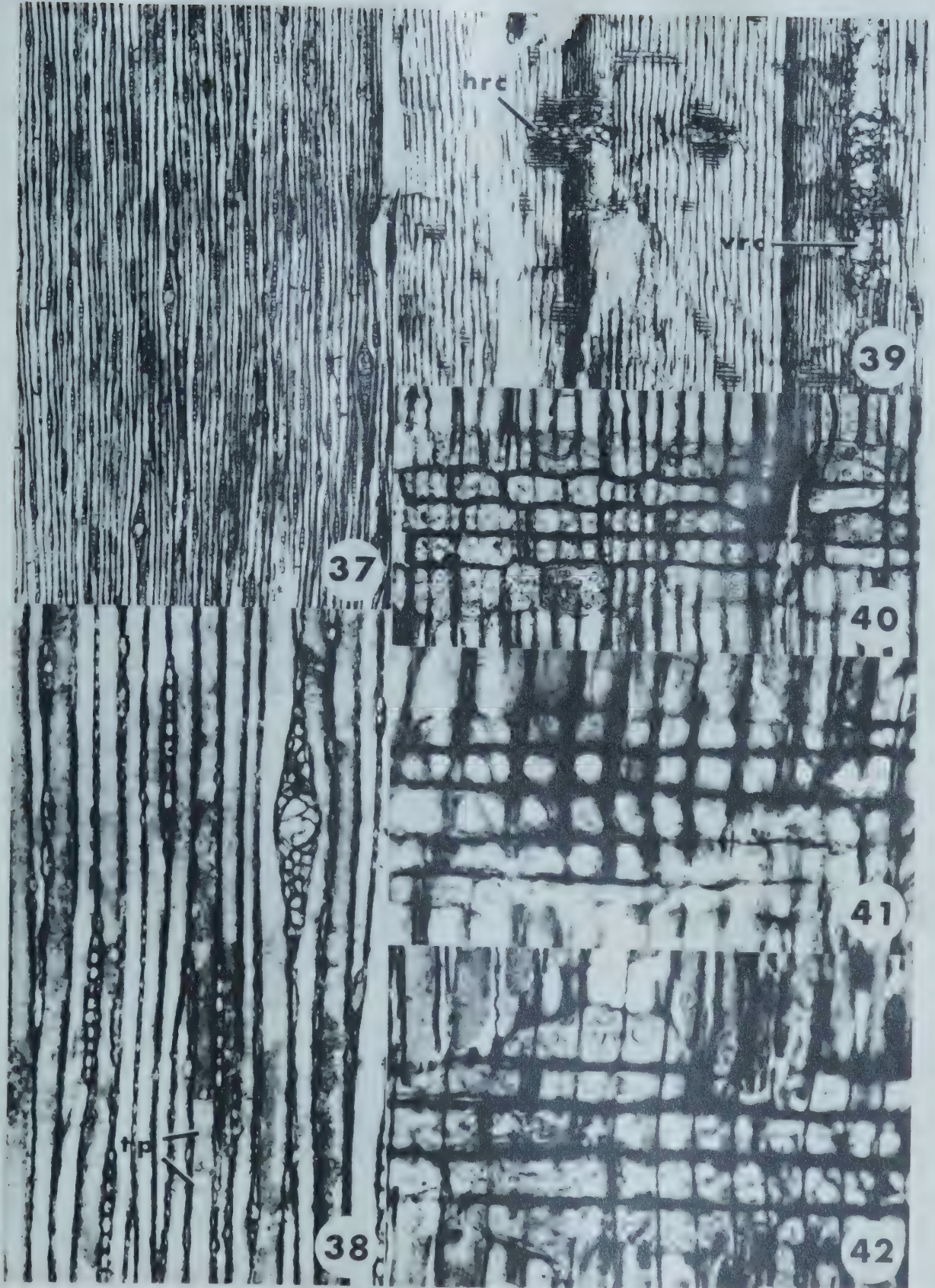
Fig. 43 - 48.   *Pinus similkameenensis*.   (fs = fascicle
                sheath).

   Fig. 43.   Cross section of a large root. The at-
              tachment of lateral roots suggests that
              roots of this kind were preserved *in situ*.
              P1143 A X 3.5.

   Fig. 44.   Triarch rootlet with a small amount of sec-
              ondary development. Note the resin canals
              at the tips of each primary xylem arm.
              P1257 I1 bot X 24.

   Fig. 45.   Longitudinal section of a young fascicle of
              pine needles showing the attached fascicle
              sheath.   P1143 F X 10.

   Fig. 46.   Cross section of a young fascicle of pine
              needles showing the quinate arrangement and
              the surrounding fascicle sheath.   P1070 C top
              X 32.

   Fig. 47.   Longitudinal section of an older fascicle of
              pine needles showing the absence of a fascicle
              sheath.   P1143 E top X 14.

   Fig. 48.   Cross section of an older fascicle of pine
              needles showing the absence of a fascicle
              sheath.   This section passed very near the
              base of the fascicle and would have included
              a fascicle sheath had one been present. P1143
              D bot X 51.

fs

fs

Figs. 49 - 53. _Pinus_ sp. (ms = microsporophyll, ps = pollen sac.)

Fig. 49. Cross sections of three pollen cones. Pl173 B bot X 20.

Fig. 50. Oblique longitudinal section of a pollen cone showing general features. Note the presence of two pollen sacs per microsporophyll. Pl254 B bot X 24.

Fig. 51. Cross section of a pollen cone containing pollen grains. Pl143 D bot X 40.

Fig. 52. Enlargement of the pollen sacs found in the specimen shown in Fig. 51. Pl143 D bot X 90.

Fig. 53. Single pollen grain showing distinct corpus and sacci. Pl143 D bot X 850.

Wood

DESCRIPTION - Taxodiaceous wood referable to this genus is
common in the chert as fragments of very large stems, with
imperceptible curvature of the annual growth rings, and as
intact twigs. In cross section (Fig. 58) the wood is seen
to lack true resin ducts, although there are frequently
rows of traumatic resin cysts. Prominent annual rings are
formed by an abrupt change in tracheid size and lignifica-
tion from spring to summer wood. Tracheids are angular in
cross section and about 70 um at their greatest diameter.

Rays are uniseriate, with occasional paired cells in
the body of the ray (Figs. 63, 66), and are very tall
(Fig. 63). Up to 80 cells have been counted in some of
the tallest rays. Ray tracheids have not been recognized.
In the cross-field are 2 to 4 taxodioid pits (Fig. 60)
with elliptical, oblique apertures.

Wood parenchyma is common (Fig. 59), and horizontal
walls of these cells are smooth or what is described by
Greguss (1955) as "indistinctly beadlike" (Fig. 66).

Circular bordered pits on the radial walls of the
tracheids are uniseriate to triseriate and opposite
(Fig. 59). The diameter of these pits, including the
border, is approximately 20 um. Crassulae are discernible
(Fig. 67), especially where paired pits occur. Smaller
circular bordered pits may occur on the tangential walls
of both early and late wood tracheids (Fig. 65). Tyloses
are found in some tracheids (Fig. 62).

DISCUSSION - The identification of this wood as taxodioid rests primarily upon the anatomical descriptions of woods of the Coniferae by Greguss (1955). Although Greguss may be criticized for the vagueness of his keys and for the construction of his phylogenetic schemes, his descriptions are basically accurate. Caution should be used, however, in that Greguss usually had only fragments of the trunks of mature trees at hand, and any attempt at comparison with his material should be made using wood of a similar origin. Little is known of the differences among the woods of trunks, roots, and twigs and the use of wood from different organs may confuse assignments.

A distinctive feature of the Taxodiaceae which is found in the fossil is the presence of smooth tangential walls of the ray cells (Greguss, 1955). This feature, Greguss notes, is also found in the Podocarpaceae and Araucariaceae, but characteristics of the horizontal and radial walls of the ray cells and of cross-field pitting readily distinguish these two families from the Taxodiaceae. Other features of the Taxodiaceae that are present in the fossil are distinct growth rings and growth ring delimitations, angularity of the tracheids in cross section, absence of resin ducts except for occasional traumatic cysts, tall, uniseriate rays, wood parenchyma, absence of spiral thickenings in tracheids, up to 3 or 4 rows of opposite pits on the radial walls of tracheids, and taxodioid pitting in the cross-field.

The Taxodiaceae is divisible into two groups based on the nature of the horizontal walls of wood parenchyma, which are primarily dentate or beadlike in <u>Glyptostrobus</u> and <u>Taxodium</u> and smooth in <u>Sequoia</u>, <u>Sequoiadendron</u>, <u>Metasequoia</u>, <u>Cryptomeria</u>, <u>Athrotaxis</u>, <u>Taiwania</u>, and <u>Cunninghamia</u>. The fossil belongs to this latter assemblage, which can further be divided into two groups; the first containing <u>Sequoia</u>, <u>Sequoiadendron</u>, and <u>Metasequoia</u>, the second, the remaining four genera. This is done by Greguss (1955) on the thickness of the horizontal walls of ray parenchyma. Although true wall thicknesses are often obscured in fossilization, the fossil appears to belong to the former. In addition, there is a tendency for the formation of very tall rays found in the former. Within the Taxodiaceae, resin cysts tend to appear in the wood of <u>Sequoia</u>, <u>Metasequoia</u>, and <u>Athrotaxis</u>, whereas cysts were not found by Greguss in other members of the family.

Distinction among the woods of <u>Sequoia</u>, <u>Sequoiadendron</u>, and <u>Metasequoia</u> is difficult, but can be done using the following features:

1. Cross-field pits in <u>Sequoia</u> have large, almost circular apertures that nearly conform to the border. In <u>Sequoia-dendron</u>, these pits have an elliptical aperture whose long axis is nearly horizontal. An elliptical aperture is found in <u>Metasequoia</u> as well, but the long axis is inclined at an oblique angle.

2. Circular bordered pits on the radial walls of tracheids

are smaller in <u>Sequoia</u> (14 - 16 um) and <u>Sequoiadendron</u>
(14 - 17 um) than in <u>Metasequoia</u> (20 - 22 um).
In both characteristics the fossil wood shows an affinity
to <u>Metasequoia</u>. An additional characteristic noted for
<u>Metasequoia</u> by Greguss, and found in the fossil, is distinct
crassulae.

It becomes apparent that the fossil wood conforms in
nearly every detail with the wood of <u>Metasequoia</u>
<u>glyptostroboides</u>.

No ray tracheids have been recognized in the fossil
wood, but this may be due to their scarcity, as they are
not common in living <u>Metasequoia</u>, or to a failure of these
thin-walled transverse tracheids to be adequately preserved.

The only obvious difference between the fossil and
<u>M. glyptostoboides</u> is the much higher rays of the former.
In this respect, the fossil is very similar to <u>Taxodium</u>
<u>distichum</u>, where rays to 60 cells in height are found. If
the ray height in the fossil is assumed to be representative
of the species and not of an environmental origin, then
ray height may indicate a relationship between extant
species of <u>Taxodium</u> and the fossil. This will be discussed
following the description of taxodioid leaves.

Leaves

DESCRIPTION - Small, coniferous leaves are found in
association with both <u>Metasequoia</u> pollen cones and the

wood described above. They occur in abundance but are rarely found to be well preserved and have not yet been found attached to twigs (Fig. 68).

The leaves are flat and measure 1.3 - 1.5 mm in width and about .35 mm in thickness. The length has not been ascertained. At the center of the leaf is a single vascular bundle which possesses a poorly defined parenchymatous bundle sheath (Fig. 71). A single mucilage duct is found on the abaxial side of the leaf between the vascular bundle and the lower epidermis. There is a notable absence of palisade mesophyll, the cortex of the leaf being comprised of large cells of an irregular shape and occasional transfusion cells (Fig. 71). A small bundle of heavily thickened fibers lies on the adaxial side of the vascular bundle and contacts the upper epidermis. Stomata have not been investigated.

Small twigs are found in association with the leaves (Fig. 68). Leaves have not been found attached to these shoots, but leaf bases on the twigs show structural similarity to the isolated leaves. Leaves are borne in a distichous manner on the shoots.

DISCUSSION - Ovoid or flattened leaves can be found in a number of conifers, but only in the Cupressaceae, Taxaceae (excluding Taxus), Cephalotaxaceae, Taxodiaceae, Podocarpaceae, and Tsuga of the Pinaceae are found just one mucilage or resin duct between the vein and the lower

epidermis (Esau, 1960). Others such as <u>Abies</u> and <u>Larix</u> have typically two ducts, one on each side (left and right) of the vascular bundle.

In the Cupressaceae, only <u>Juniperus</u> has needle-like leaves, others having scale-leaves. Leaves of <u>Juniperus</u> are similar to the fossil leaves except that there is a distinct palisade layer on the adaxial side of the leaf. <u>Tsuga</u>, <u>Podocarpus</u>, and all genera of the Taxales show a well developed palisade layer and prominant bundle sheath.

A remarkable resemblance exists between the fossil leaves and leaves of <u>Taxodium</u> (Figs. 70 - 73). Other taxodioid genera such as <u>Sequoia</u> and <u>Cunninghamia</u> have a palisade layer, while <u>Cunninghamia</u> and <u>Metasequoia</u> typically have more than one mucilage duct.

Although the resemblance of the fossil leaves to leaves of <u>Taxodium</u> is marked, there is a close association of these fossil leaves with other remains assignable to <u>Metasequoia</u>. The distichous arrangement of leaf bases on associated vegetative shoots which are believed to have borne these leaves is also strong evidence for their referral to <u>Metasequoia</u>.

Since pollen cones, wood, and leaves have been found in close association with one another, and there is apparently only one type of each organ present, it is very probable that they all represent different organs of the same species. However, they show a combination of features of two modern genera: Pollen cones are like

those of Metasequoia; wood is basically like that of Metasequoia, but shows some resemblance to Taxodium; and the leaves are most like those of Taxodium. Since these organs are considered to represent a single species, the fossil may provide information on the evolutionary relationships between Taxodium and Metasequoia.

Arnold and Lowther (1955), when reporting on their controversial genus Parataxodium, reviewed the history of Sequoia, Metasequoia, and Taxodium. It appears that Sequoia was first to become differentiated from a basic ancestral stock during the early Mesozoic. Two evolutionary lines resulted: one involving species such as Sequoia jeholensis, S. affinis, and S. sempervirens; the other, according to Arnold and Lowther, including species such as their Parataxodium wigginsii. From this latter group they suggest Metasequoia evolved during the Upper Cretaceous and Taxodium during the latest Cretaceous or early Tertiary.

In view of the possible evolution of Metasequoia followed shortly by Taxodium during the Upper Cretaceous, it is reasonable to expect that a complex of closely related plants including early forms of Metasequoia and Taxodium existed during the early Tertiary. These forms may not yet have evolved all the characteristics of their modern counterparts and may have had many primitive characteristics in common.

The species presented in this study appears to have been a part of this complex. Reproductively the fossil is

apparently very close to Metasequoia glyptostroboides.
Until seed cones can be found and examined, it will be
uncertain as to the true reproductive relationships.
Vegetatively, however, the fossil has not yet developed
all of the characteristics of modern Metasequoia. The
wood of the fossil has evolved basically the qualities of
Metasequoia, although ray height is more like that of
Taxodium. Leaves, however, are anatomically similar to
those of Taxodium and have not developed characteristics
of Metasequoia leaves. An important point of similarity
between the fossil and Metasequoia is the arrangement of
the leaves. Both the scale-like leaves of the pollen
cones (Rothwell, 1975) and the leaves borne by the vegeta-
tive shoots are produced in a distichous manner which is a
characteristic of Metasequoia.

It should be noted that basic differences between the
leaves of both the fossil and Taxodium and those of
Metasequoia are an increased number of mucilage ducts,
a slight development of a palisade mesophyll, and a
generally greater width. There is a tendency toward
formation of a palisade layer in Taxodium and the fossil.
Both the formation of palisade mesophyll and the increased
number of mucilage ducts in Metasequoia may be a function
of the much greater leaf size attained by Metasequoia.
Only the very smallest Metasequoia leaves approach the size
of the fossil leaves. However, even the smallest of
Metasequoia leaves studied had three mucilage ducts throughout

most of their length, whereas none of the fossil leaves were found to have more than one duct.

Despite some vegetative differences with Metasequoia glyptostroboides, the fossil species is here referred to the genus Metasequoia. Although close similarities are indicated, the true relationships of the fossil to M. glyptostroboides will be uncertain until further study of the vegetative remains is completed and seed cones have been found. Comparisons with other fossil species of Metasequoia must also await further investigation. However, the lack of preserved anatomical and reproductive detail in other fossil forms may not allow useful comparisons.

The combination of features found in the fossil implies a lesser degree of distinction between Taxodium and Metasequoia in the early Tertiary than may have been previously recognized. Morphologically Metasequoia is readily distinguishable from Taxodium in sediments of that age, but the fossil presented here reveals that anatomical differences are less pronounced. Since that time these forms have evolved into unique genera.

Figs. 54 - 57. *Metasequoia* sp. (md = mucilage duct, ms = microsporophyll).

Fig. 54. Cross section of a pollen cone showing general features. P1249 C top X 25.

Fig. 55. Cross section of a pollen cone showing the prominent mucilage duct present in each microsporophyll. P1195 E X 30.

Fig. 56. Oblique section of a pollen cone showing the attachment of three pollen sacs per microsporophyll (top). Note also the large mucilage duct in each microsporophyll. P1209 I top X 29.

Fig. 57. Pollen grains found in the specimen shown in Fig. 56. Note that the grains are spherical and papillate. P1209 I top X 265.
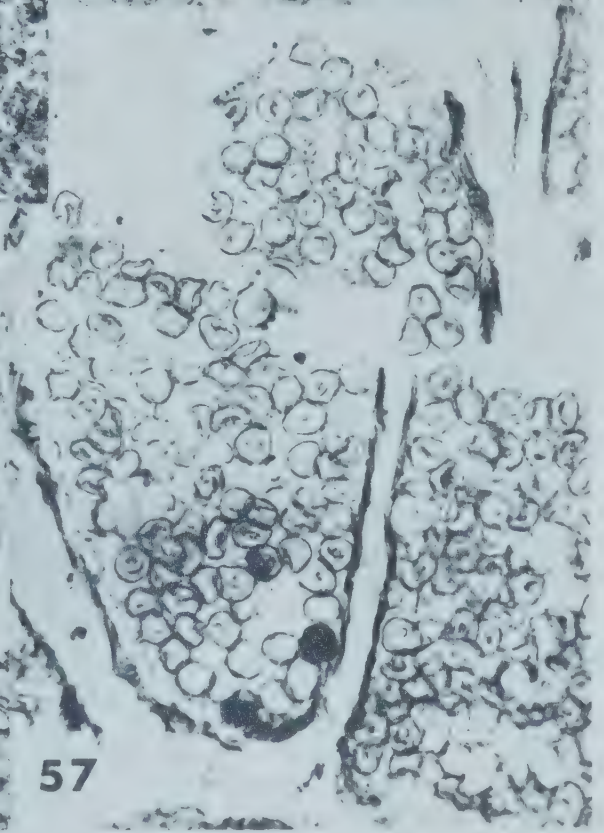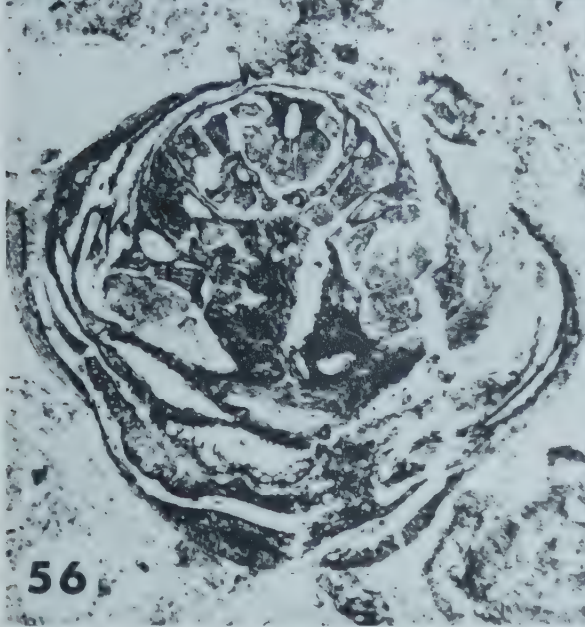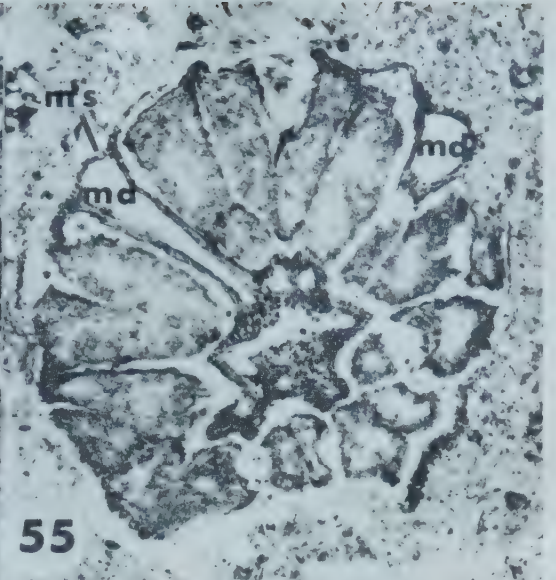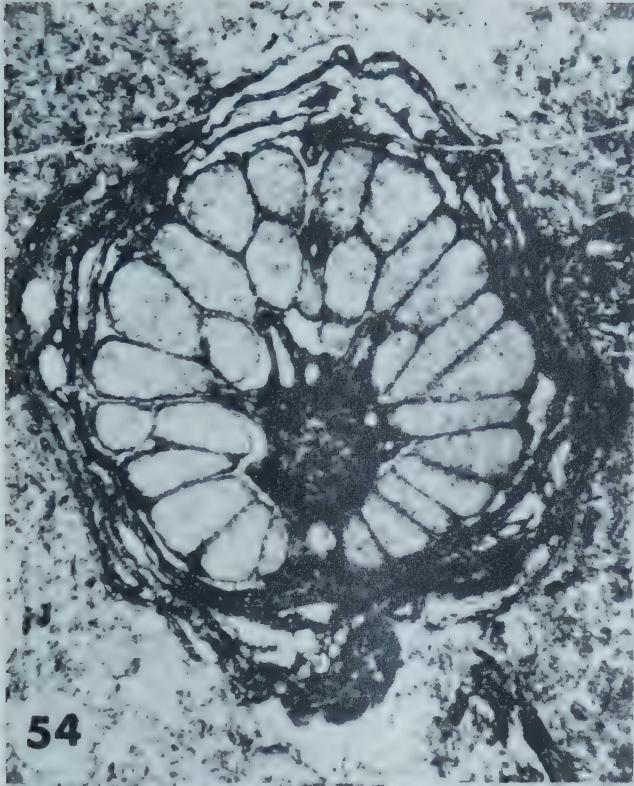
Figs. 58 - 62. *Metasequoia* sp. Cross and radial sections
of wood. (trc = traumatic resin cyst).

Fig. 58. Cross section showing the angularity of the
tracheids and the abrupt change from early
to late wood. Note the row of traumatic
resin cysts in the early wood to the left.
P1102 E X 29.

Fig. 59. Radial section of wood showing general fea-
tures. Note the primarily bi- and triser-
iate, opposite pitting. P1102 E X 25.

Fig. 60. Radial section showing cross-field pitting.
The pits appear as slits inclined at an
oblique angle. P1102 E X 175.

Fig. 61. Traumatic resin cysts in radial view.
P1102 E X 110.

Fig. 62. Radial section through several tracheids
that have been occluded by what may be tyloses.
P1102 E x 122.

58

59

60

61

62

trc
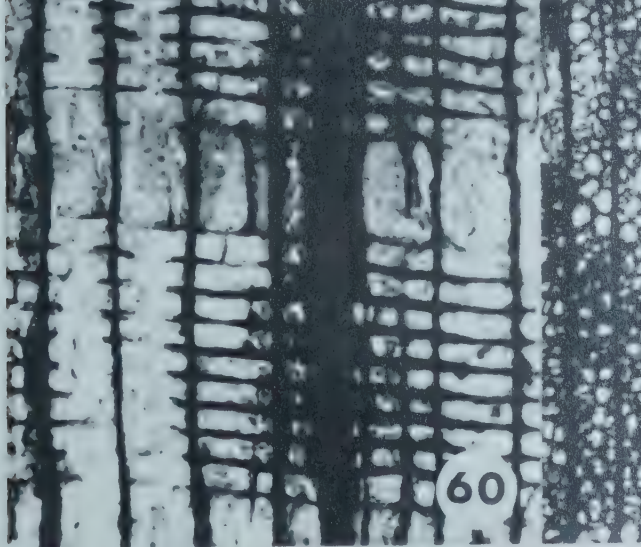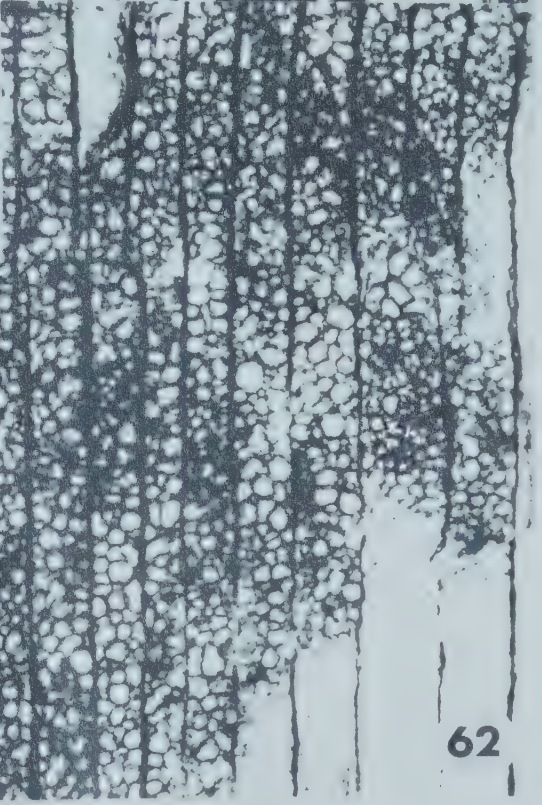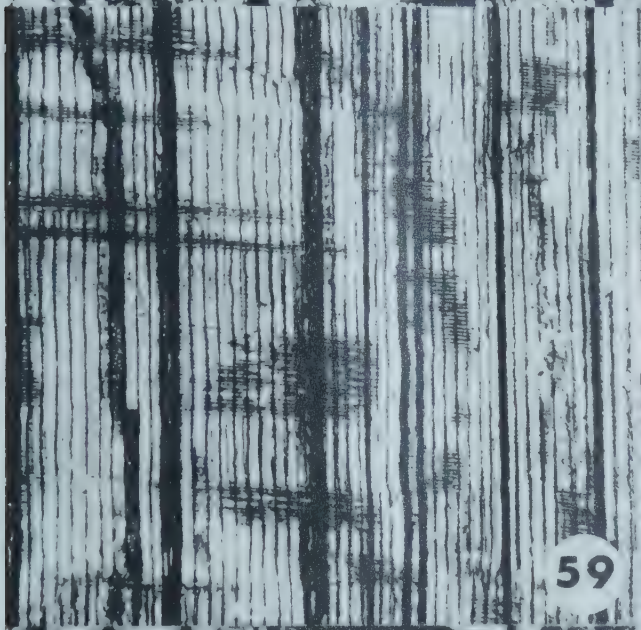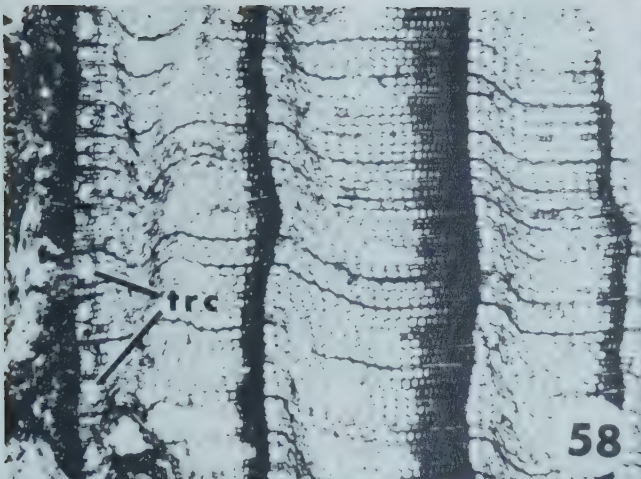
Figs. 63 - 67. *Metasequoia* sp. Radial and tangential sec-
tions of wood. (cr = crassulae, tp = tan-
gential pits).

Fig. 63. Tangential section of wood showing general
features. Note the variation in ray height
from one to over 60 cells (the tall ray to
the left is 80 cells high). Pl102 E X 62.

Fig. 64. Tangential section showing wood parenchyma.
Note the resinous contents of the cells.
Pl102 E X 62.

Fig. 65. Pitting on the tangential walls of the trach-
eids. Pl102 E X 80.

Fig. 66. Closeup of the wood parenchyma cells shown in
Fig. 64. Note the smooth to slightly bead-
like horizontal walls. Note also the paired
cells in the body of the ray at the lower
left. Pl102 E X 220.

Fig. 67. Radial section showing crassulae between
pairs of pits. Pl102 E X 380.

63

64

65

66

67

tp

cr
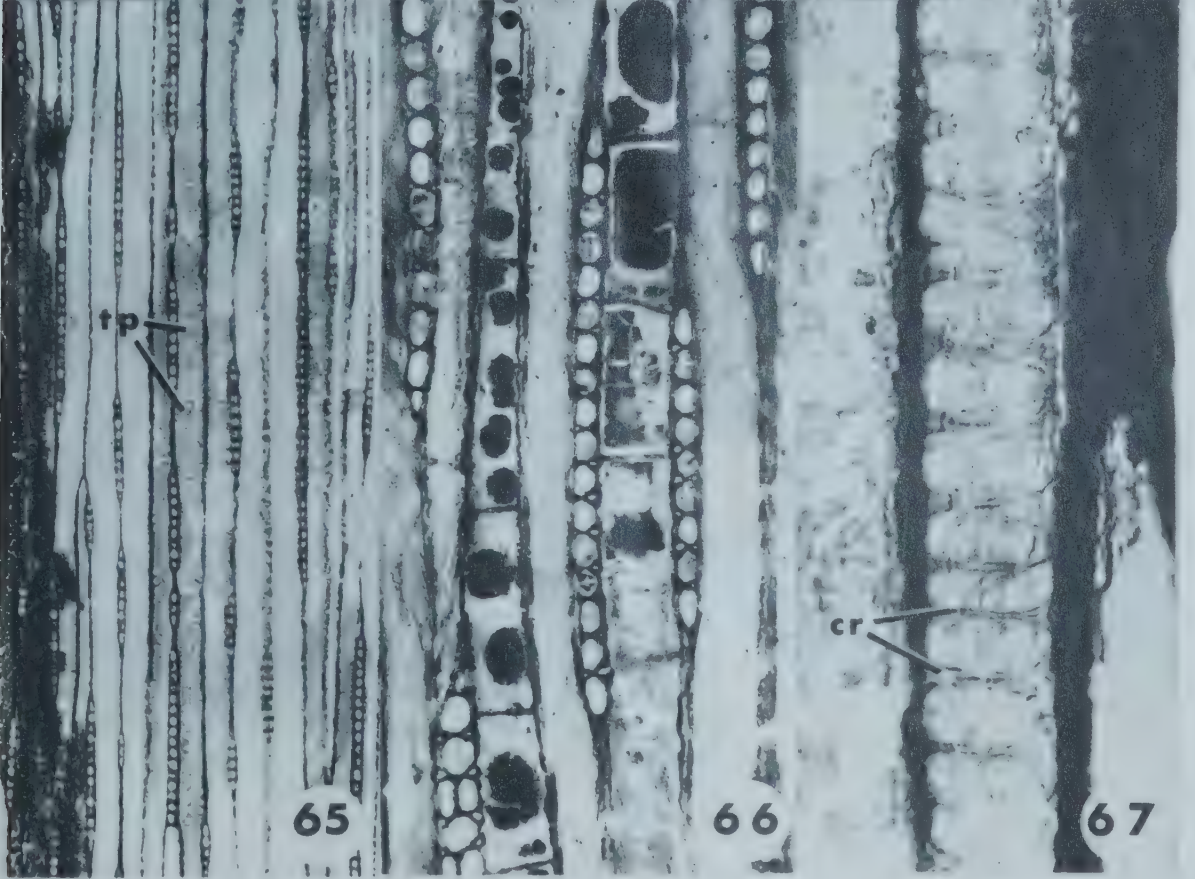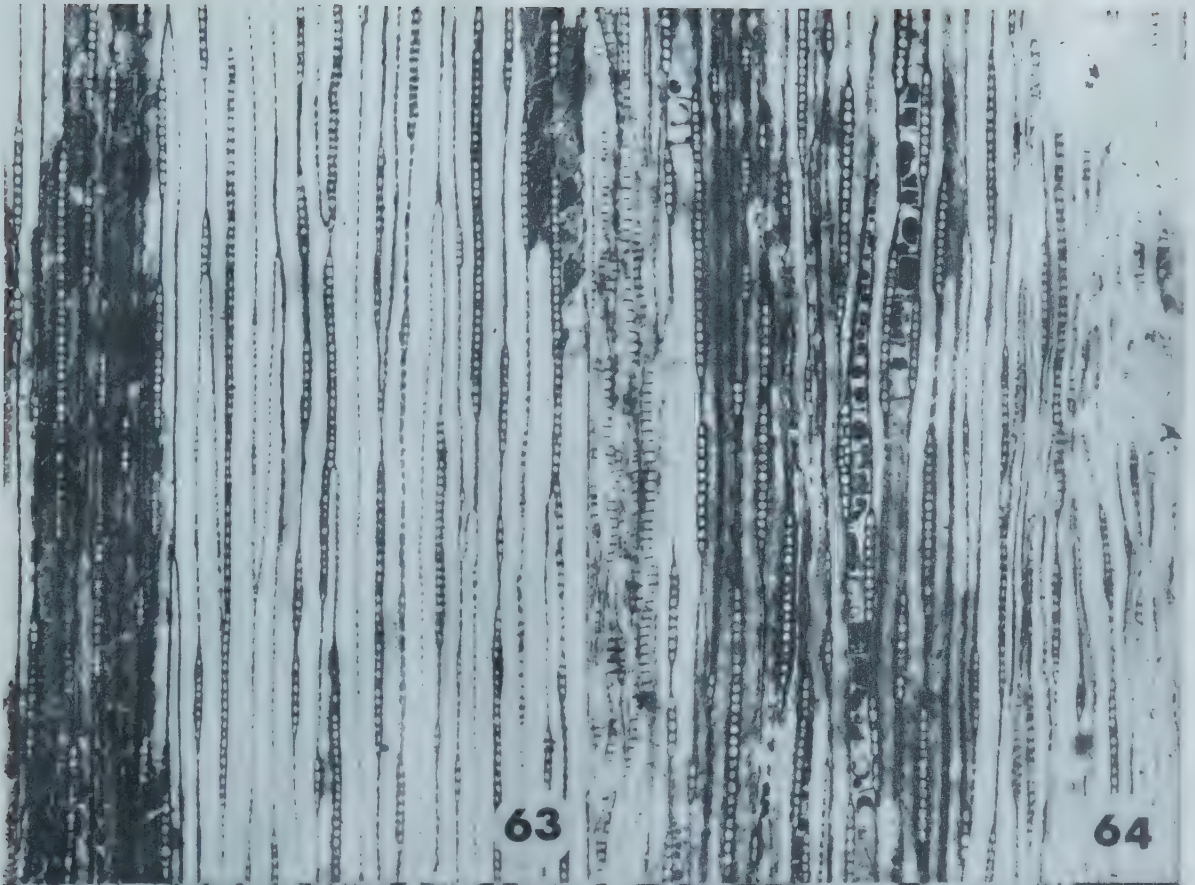
Fig. 68 - 73. *Metasequoia* sp. (lb = leaf base, md = mu-
cilage duct, scl = sclerenchyma, tc = trans-
fusion cell, x = **xy**lem).

Fig. 68. Cross sections of a leaf and a small twig.
Note the degree of structural similarity
between the leaf and the leaf bases found on
the shoot. Note also the opposite arrange-
ment of leaf bases on the shoot. Pl095 B
bot X 55.

Fig. 69. Cross section of leaf showing general fea-
tures. Note the single mucilage duct loca-
ted between the vascular bundle and the lower
epidermis. Pl095 B top X 64.

Fig. 70. Cross section of a leaf. Pl095 D top X 84.

Fig. 71. Closeup of the central portion of the leaf of
Fig. 70. showing the vascular bundle mucilage
duct, abaxial bundle of sclereids, and trans-
fusion cells. Pl095 D top X 180.

Fig. 72. Cross section of the leaf of *Taxodium disti-
chum*. Compare with Fig. 70. X 106.

Fig. 73. Closeup of the portion of the leaf of Fig. 72.
Compare with Fig. 71. X 235.

Figures 68–73. Labels: lb, scl, x, c, tc, md. Figure numbers 68, 69, 70, 71, 72, 73.
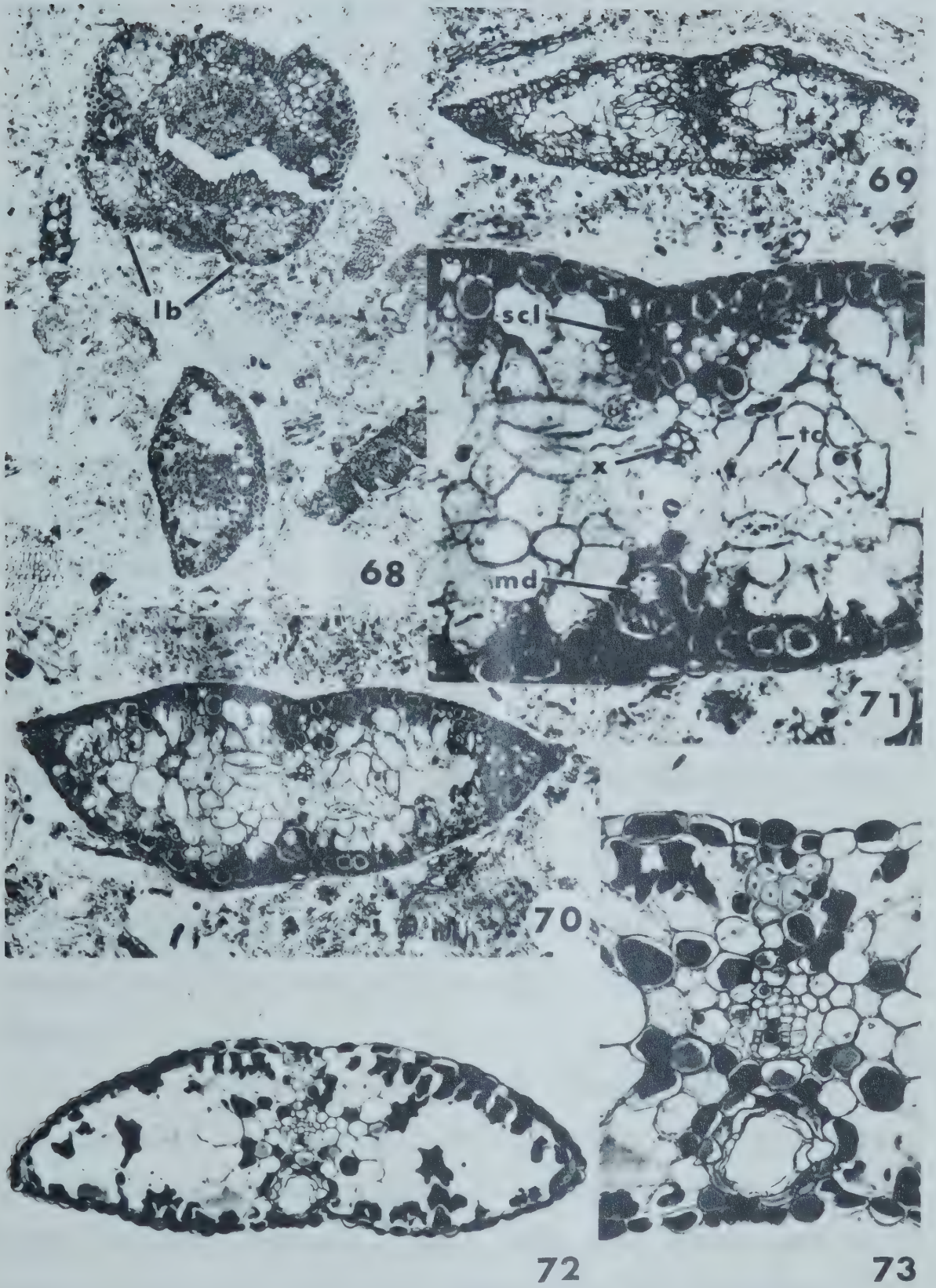
Class: Angiospermae

Sub-Class: Dicotyledonae

Order: Rosales

Family: Rosaceae

Paleorosa similkameenensis, gen. et sp. nov. (Figs. 74-87)

Over 100 flowers assignable to this species were found
scattered throughout several blocks of chert and in associa-
tion with Pinus, Eorhiza, palms, and the remains of other
angiosperms. Their discovery is of paramount importance
in view of the rarity of identifiable flowers and other
angiospermous reproductive organs in the fossil record and
the resulting lack of knowledge of reproductive mechanisms
of early angiosperms. There are some descriptions and
reports of flowers as compressions found in the literature
(Knowlton, 1917; Berry, 1913, 1916, 1930; MacGinitie, 1953;
Becker, 1973; Krassilov, 1973; etc.), but their poor pre-
servation rarely allows accurate identification. Recent
work by Crepet, Dilcher, and Potter (1974, 1975) has,
however, revealed remarkable details of some compressed
flowers.

Some of the more spectacular fossil flowers have
been found in the Oligocene, Baltic Amber. Extensive work
has been done on these fossils (Goeppert and Menge, 1883;
Conwentz, 1886; Czeczott, 1960), with many genera such as
Quercus, Castanea, Acer, and Sambucus being recognized.
Studies of other ambers (Hurd, Smith, and Durham, 1962;

Miranda, 1963; Langenheim, 1964; McAlpine and Martin, 1969)
have revealed few flower parts.

Permineralized flowers have previously been found only
in the Upper Cretaceous of Japan (Stopes, 1909, 1910; Stopes
and Fujii, 1911) and in the Deccan Intertrappean series,
Eocene in age, of India. Cretovarium japonicum was described
from fragmentary remains by Stopes and Fujii as possibly
liliaceous. Specimens of five species of petrified flowers
have been described from the Mohgaon-Kalan beds of India.
They are Sahnianthus parijai (Shukla, 1944; Chitaley, 1950,
1955), Sahnipushpam shuklai (Shukla, 1950; Verma, 1956;
Parkash, 1956; Prakash and Jain, 1964; Chitaley, 1964),
Chitaleypushpam mohgaoense (Paradkar, 1973), Deccananthus
savitrii (Chitaley and Kate, 1974), and Raoanthus inter-
trappea (Chitaley and Patel, 1975). Unfortunately, accurate
reconstructions of these flowers have not been made and
affinities are uncertain.

The flowers described here are by far the best
preserved and most completely understood of all permineralized
flowers known to date. Superb preservation, rarely possible
for soft floral parts, has permitted reconstruction and made
it possible to identify the fossils as members of the family
Rosaceae. These fossil flowers, which are the oldest known
rosaceous flowers, have provided valuable information on
early floral evolution in this family.

Basically two different stages of floral development
are seen. One is found as a somewhat immature form, where

the flowers appear to be buds (Figs. 76,77,78,84); the other, a slightly larger, more mature form (Figs. 75,81,83) has young seeds but lacks petals and stamens. On considering similarities in structure and studying two specimens which possessed both young seeds and stamens (Fig. 83), it was concluded that these two types represent different developmental stages of a single species. Preservation is often less complete in the immature form. The presence of a variety of developmental forms, all found detached from the parent plant, could be the result of trauma experienced during the influx of hot, mineral rich water prior to permineralization. This can also account for the lack of later stages of fruit development, for only those stages borne by the dying plant would be available for fossilization.

Each flower (Fig. 74) is borne on a pedicel to which is attached a single bract. A striking feature is the floral cup which is comprised of the fused bases of the sepals, petals, and stamens. The flowers are pentamerous, with alternate insertion of the sepals and petals. Stamens are indefinite in number, varying from 13 to 19. The five carpels are free and each contains two erect ovules. The complete perianth and included stamens suggest entomophilly.

SYSTEMATIC DESCRIPTION:

Generic diagnosis: Paleorosa gen. nov.

Flowers permineralized, bisexual, actinomorphic. Five sepals and five petals inserted alternately, many

Fig. 74. Reconstruction of _Paleorosa similkameenensis_ showing a median longitudinal section of the flower. Hairs that cover carpels and styles have been omitted. For further explanation of details see text.

1 mm
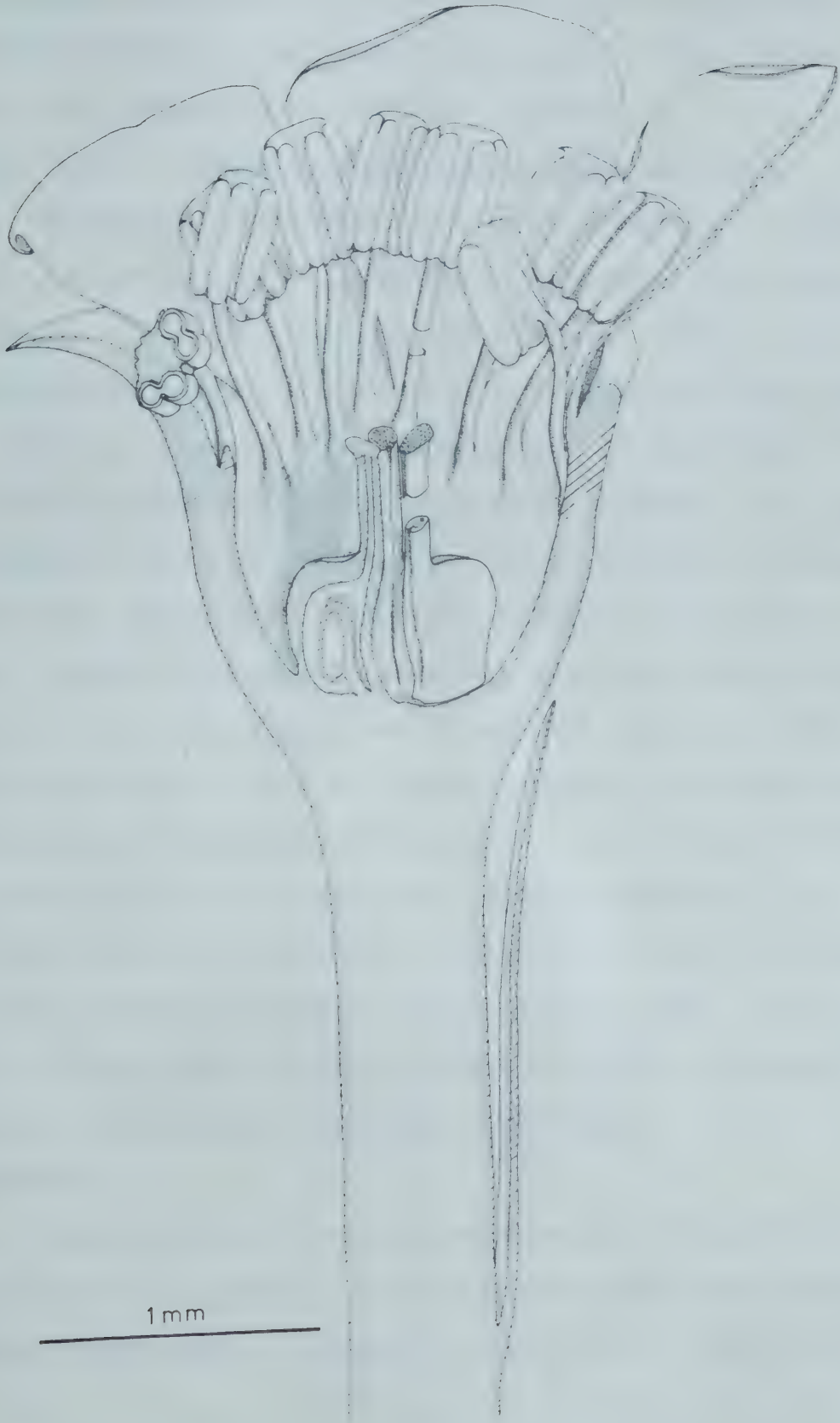
stamens, five free carpels. Floral cup surrounding
apocarpous gynoecium. Ovules 2 per carpel, collateral,
basally attached, erect, and anatropous. Fruit, mature
seeds, and vegetative structures unknown.

Type species: Paleorosa similkameenensis sp. nov.

Flowers as described in generic diagnosis. Pedicel
1.2 - 1.7 mm long, 0.4 - 0.5 mm in diameter, with single
bract 1.0 - 1.6 mm long attached at base. Floral cup 0.5 -
1.8 mm in diameter, 0.5 - 1.4 mm deep from point of insertion
of petals to base of cup. Sepals 0.5 - 0.8 mm long. Size
of petals unknown. Number of stamens variable, 13 - 19,
filaments 0.3 - 0.4 mm long, 0.1 mm in diameter. Anthers
bilocular, dorsifixed, 0.5 - 0.6 mm high, 0.2 - 0.4 mm
wide. Carpels pubescent, inserted opposite sepals, borne
at base of floral cup, fused to wall of cup up to level of
ovular insertion, free at ventral margins. At stages of
early seed development, carpels 0.7 - 1.1 mm high, 0.4 -
0.5 mm wide, 0.4 - 0.5 mm deep. Style terminal, 1.1 - 1.3
mm long, 0.2 mm in diameter, with hollow center. Dorsal
vascular bundle of carpel continues into style. Ovules
0.5 - 0.9 mm long, 0.2 mm in diameter basally attached,
erect on funiculus 0.1 mm long, anatropous.

Holotype:

University of Alberta Paleobotanical Collection (UAPC)
chert block No. P1122I. Cross section from which serial
sections were made. Slides Nos. 2545-2550. Fig. 75.

Paratypes:

UAPC No. P1118E bot. Longitudinal section, slides Nos. 2555-2556. Figs. 77,87. UAPC No. P1119J bot. Oblique longitudinal section, slides Nos. 2543-2544. Figs. 80,84. UAPC No. P1123B top. Longitudinal section, slides Nos. 2551-2554. Fig. 76. UAPC No. 1143E bot. Oblique cross section, slides Nos. 2557-2580. Figs. 81, 82, 85.

Type Locality:

On the east bank of the Similkameen River, 8.4 kilometers SSW of Princeton, British Columbia. Allenby Formation, Middle Eocene.

Derivation of Name:

Paleo, Latin for ancient; rosa, rose. Specific epithet from type locality on Similkameen River.

DESCRIPTION - The pedicel is rather short and has a single, small bract of about equal length attached to its base (Fig. 76).

Lower portions of the sepals, petals, and stamens are fused to form a floral cup 0.5 - 1.8 mm in diameter and 0.5 - 1.4 mm high (Figs. 73,77). Sepals appear to be continuous with the floral cup, which thus resembles a five-lobed calyx tube. Petals and sepals are inserted alternately. Since only the flowers in bud possessed petals, dimensions of the petals could not be accurately measured. However, their length is estimated at 1.5 mm,

with a width of about the same. The floral cup is
vascularized by ten major bundles (Fig. 75) reflecting
the pentamerous structure of Paleorosa. The quality of
preservation in this part of the flower did not permit a
study of the vascularization of sepals and petals. The
wide range in measurements of floral parts is, to a large
part, due to the different developmental stages of the
flowers. Measurements approximately midway between the
extremes would most nearly represent dimensions of a flower
at anthesis.

Stamens consist of rather large (0.5 x 0.3 mm)
anthers and short (0.4mm) filaments (Fig. 77,79). The
anthers were apparently not elevated far beyond the perianth,
are dorsifixed, and possess a broad connective. Figure 87
shows the discontinuity of the septum between adjacent
pollen sacs, forming a bilocular condition. Stamens are
of a variable number. Counts from flowers in bud, from
which no stamens could have been lost, vary from 13 to 19.
A few of the anthers contain the remains of pollen grains
(Figs. 77,79,87). These pollen grains are not well pre-
served and may have been immature at the time of permineral-
ization. However, Boneham (1968) was able to recover very
little dispersed pollen from the layers of chert and what
he did find was poorly preserved. Physical factors at the
time of fossilization, therefore, may have inhibited the
preservation of pollen grains.

Five pubescent carpels are inserted at the base of

the floral cup, opposite the sepals. A single specimen, which is similar to the rest of the flowers in all other respects, has six carpels and presumably reflects variability within the species. The carpels are free from one another, but are fused to the floral cup up to the level of ovular insertion (Fig. 75). Often the ventral margins of adjacent carpels appear fused (Fig. 75), but a close examination reveals a continuous epidermis surrounding each carpel. In the central region there appears to be some type of material, but it is not certain whether it is detrital, is made up of a mat of hairs, or is a raised torus, since no cellular detail has been preserved.

Each of the five carpels is supplied by a dorsal vascular bundle, two ventral or wing bundles, and a number of vegetative bundles (Fig. 81). Only the dorsal bundle continues into the style. Although a vascular strand is cearly visible in the funiculus, it was not possible to see the origin of the ovular supply.

The styles extend to the upper level of the floral cup (Figs. 83,84) and, in cross section, are hollow with a dorsal bundle and a well defined ventral suture (Fig. 86). This suture is evident in both the style and the carpel body (Fig. 82). Although not well preserved, the stigmatic surfaces appear to have been simple.

Ovules are two per carpel, basally attached, erect, and anatropous. The two integuments (Fig. 82) are interpreted as free, for they are sometimes separate from one

another. Flowers that show structural preservation of the
carpels are in a post-fertilization state of development,
but have not yet undergone fruit formation. Although there
is some tissue preserved in several of the developing seeds,
embryos have not been recognized. Considering the state of
maturation of these flowers, this tissue may represent
endosperm.

Each carpel contains ovules which appear equally well
developed, and likely formed a two-seeded follicle.

DISCUSSION - A floral cup can be found in a large number of
families and can be broadly interpreted as a fusion of basal
portions of sepals, petals, and stamens (van Tieghem, 1875;
Eames, 1931; Jackson, 1934; Wilson and Just, 1939;
MacDaniels, 1940; Cronquist, 1968). It was once widely
believed that the floral cup was not appendicular but
receptacular in origin (Prayer, 1857; Rydberg, 1898; Krause,
1913, Judson, 1929, etc.). Receptacular floral cups,
however, are now considered to be the case in only a few
families such as the Eupomatiaceae (Magnoliales),
Calycanthaceae (Laurales), Santalaceae (Santales), and
perhaps Cactaceae (Caryophyllales) (Boke, 1964; Cronquist,
1968). In the Rosaceae, the genus Rosa has been shown to
possess a floral cup that is in part both appendicular and
receptacular (van Tieghem, 1878; Bonne, 1928; Jackson, 1934).
Though detailed study of the vasculature is necessary in
order to determine the type of origin, a cup formed of a

hollowed receptacle is the less common condition and is often characterized by having carpels borne on the walls of the cup. Since there is apparently no carpellary component, the floral cup of Paleorosa is interpreted as appendicular.

Families containing members with floral cups that could be considered similar to those of this fossil include: Lauraceae, Monimiaceae (Laurales); Aristolochiaceae (Aristolochiales); Hamamelidaceae (Hamamelidales); Ebenaceae, Styrocaceae (Ebenales); Loasaceae (Violales), Moringaceae (Capparales); Rosaceae, Saxifragaceae (Rosales); Myrtaceae, Lythraceae, Onagraceae, Melastomataceae (Myrtales); Staphyllaceae (Sapindales); Celastraceae (Celastrales); Rhamnaceae, Vitaceae (Rhamnales); and Caryophyllaceae (Caryophyllales).

Many wholly epigynous families have not been included because they are generally considered rather advanced and have evolved from families which possess members with superior gynoecia. Formation of a floral cup and the resulting condition of perigyny have been interpreted as a step toward epigyny where the carpels and floral cup have fused (Cronquist, 1968). Epigyny, however, is not necessarily dependent upon ancestral perigyny, but may arise through adnation of free floral parts to the carpels. This may have occurred in families such as the Rubiaceae and Campanulaceae, for Cronquist (1968) states that in these two families "... there is no history of a separate hypanthium.".

In nearly all families listed above, the development of a syncarpous gynoecium preceded the development of a floral cup. Only a few families such as the Rosaceae, Saxifragaceae, and Monimiaceae have members with both an apocarpous gynoecium and a floral cup. Of these, only in the Rosaceae are found all other features of the fossil: pentamerous and actinomorphic perianth, numerous stamens of an indefinite number, five free carpels, and two ovules per carpel.

Although the genera of the Rosaceae have been isolated in smaller families (Payer, 1857; Bessey, 1915; etc.), the Rosaceae has been recognized as a very natural group by the majority of taxonomists (Lawrence, 1951; Hutchinson, 1973; Robertson, 1974; etc.). In such a closely knit family, however, tribal limits are more difficult to deal with. The Rosaceae has been variously divided into sub-families and tribes by such authors as de Candolle (1825), Bentham and Hooker (1865), Focke (1894), Rydberg (1908), Schulze-Menz (1964), and Hutchinson (1964). The most recent classification has been prepared by Robertson (1974), whose system of four sub-families and 15 to 17 tribes is the system used here. Robertson discusses the treatment of the genus Holidiscus, but does not give it a definite position. This genus is considered here as belonging to a distinct tribe, the Holodisceae, of the sub-family Spiraeoideae (Focke, 1894; Schulze-Menz, 1964). The sub-family Maloideae is considered as consisting of a single tribe and is not split into the

tribes Crataegeae and Sorbeae, a division which Robertson

(1974) says, "... may not best reflect generic relationships.".

Within the Rosaceae, tribes which include members with

five carpels and two ovules per carpel are the Osmaronieae

(Amygdaloideae), Maleae (Maloideae), Spiraeeae, Holodisceae,

Quillajeae, Sorbarieae (Spiraeoideae), and Ulmarieae

(Rosoideae). A difficulty arises in attempting to immediately

assign Paleorosa to one of these tribes, since it is the

nature of the fruit that basically determines affinities.

With the exception of the Osmaronieae, which appears to be

highly modified, any of these tribes might accommodate

Paleorosa, since its fruit is unknown.

From a phylogenetic point of view, the Rosaceae is a

very important family. It is believed that families such

as the Saxifragaceae, Leguminosae and, indeed, all families

of the Rosales find their origin directly or indirectly in

the Rosaceae (Cronquist, 1968). Furthermore, all orders of

the sub-class Rosidae can be traced to the Rosales (Bessey,

1897, 1915; Cronquist, 1968). The sub-class Asteridae may

be derived from certain members of the Rosidae (Bessey, 1897,

1915; Cronquist, 1968; Takhtajan, 1969). The Rosidae

contains more than one-third of all species of dicotyledons.

The origin of this very prolific group of angiosperms appears

to lie within the Rosaceae, and the necessity of understanding

evolution within this family is clear. Paleorosa represents

one of the oldest fossil members of this family, and is the

oldest known fossil flower that can be positively identified

as rosaceous.

Spiraeoid tribes are considered ancestral within this family, but opinions vary as to the nature of the ancestral type. It has been proposed that the many-seeded follicle of most spiraeoids was derived from an ancestor within the Dilleniaceae or a similar family (Bailey and Swamy, 1951; Eames, 1961; Hutchinson, 1964), although the sub-classes Dilleniidae and Rosidae have been considered as parallel lineages with their origins in the Magnoliidae (Cronquist, 1968). A more recent theory holds that the primitive rosaceous carpel has but two seeds and represents an independent line of evolution with its origin in the Magnoliales (Sterling, 1964c, 1966a, c). Although Sterling (1969) and Eyde (1975) have found evidence for a reduction from many- to few-seeded carpels among extant, multiovulate spiraeoids, a biovulate condition is found in members of the Quillajeae and Sorbarieae which are most closely alligned with magnoliaceous groups (Sterling, 1966c).

Studies of rosaceous floral anatomy by such authors as Maximowicz (1879), Juel (1918, 1927), Bonne (1928), and Sterling (1964a, b, c, 1965a, b, c, 1966a, b, c) have contributed to a better understanding of relationships within the family. Some of the evolutionary trends proposed for the Rosaceae are an increase or decrease in the basic numbers of five carpels and two ovules per carpel, fusion of the two integuments, intercarpellary fusion, carpel to floral cup fusion, and fusion of wing and ovular vascular

bundles to reduce the carpellary supply from five to three major bundles.

The most primitive members of the family according to these criteria are to be found within the tribes Quillajeae and Sorbarieae. Although floral structure is similar in both tribes, the Quillajeae is considered the more primitive of the two on the basis of vegetative features and a tropical distribution (Hutchinson, 1964). Sterling (1966c) has pointed out, however, that in neither the Quillajeae, nor in any other tribe, is there found a species which combines all of the primitive features. All have become advanced in one or more ways.

Sterling (1966b, c) and Cronquist (1968) have noted that the position of the ovules may be important in determining relationships within the Rosaceae. In all of the Maloideae, ovules are basally attached, erect, anatropous, and apotropous (micropyle directed toward base of locule). In all other tribes, with few exceptions, ovules are apically attached, pendulous, anatropous, and epitropic (micropyle directed toward apex of locule), or can be derived from this condition (e.g., Dryadeae have erect ovules, but a basally inserted style). These exceptions are notably found in Quillaja and Vauquelinia of the Quillajeae and Gillenia and Spiraeanthus of the Sorbarieae.

Chromosome numbers also support recognition of the Maloideae as a distinct line. Base chromosome numbers of the Rosoideae are 7, 8, and 9; the Spiraeoideae, 8, 9, and

10; the Amygdaloideae, 8; and the Maloideae, 17 (Robertson, 1974). The only exception to these rules is a base number of 17 for Quillaja brasiliensis (Bolkhovskikh et al., 1969).

The possible relationships between the Quillajeae and Sorbarieae and the Maloideae have been discussed by van Tieghem (1875), Maximowicz (1879), Juel (1918, 1927), Bonne (1928), and Sterling (1966c). Differences are basically in the nature of the fruit, which is pomoid in the Maloideae and follicular in the Quillajeae and Sorbarieae. Chemo-taxonomic evidence is also in agreement with relationships among these tribes (Challice, 1974).

The evidence presented suggests that there are two major lines of evolution within the Rosaceae. Both appear to have their origins within the Quillajeae and Sorbarieae, with one line deriving the Maloideae, the other, the bulk of the other three sub-families. Ovular position appears to be a fairly accurate indicator of affinities.

Thus, considering current views of the evolutionary trends in the Rosaceae, Paleorosa appears primitive in all observable features. Carpels are five (rarely 6) and free, ovules are two per carpel, integuments are two and apparently not fused, there is no intercarpellary fusion, and fusion of the carpels to the floral cup is minimal.

Sterling (1966c) notes that fusion of the ventral margins of adjacent carpels, without similar fusion of the carpels to the floral cup, is generally the trend in higher spiraeoids. Retention of free ventral margins of adjacent

carpels, with progressive fusion of the carpels to the floral cup, is a trend found in the Maloideae. There is enough fusion of the carpels to the floral cup in Paleorosa to suggest a relationship with the Maloideae.

Paleorosa also has basally attached, erect ovules, which further supports its alliance with the Maloideae. Considering the slight degree of fusion (up to ovular insertion), however, it is unlikely that the fruit could have been a pome. It is more likely that the fruits were follicular as in the Quillajeae or Sorbarieae. Until fruits are found, a decision as to where Paleorosa fits among the groups must be made utilizing data from the living members that show comparable floral structure.

Flowers with similar features are found in Pyracantha of the Maloideae, Vauquelinia of the Quillajeae, and Gillenia trifoliata and Spiraeanthus of the Sorbarieae. However, as noted earlier all are modified in one or more ways. Paleorosa has less fusion of its carpels to the floral cup than does Pyracantha, which is possibly the least advanced member of the Maloideae. In Vauquelinia there is considerable intercarpellary fusion. Spiraeanthus has also undergone intercarpellary fusion and has ovules with single integuments. Gillenia trifoliata is possibly least modified, with some fusion of ventral carpellary margins, but lacking carpel to cup fusion. The situation is reversed in Paleorosa. Only those genera with erect ovules have been discussed. However, spiraeoids with pendulous ovules show similar

structural modification.

An advanced character that is found in all Quillajeae and Sorbarieae, but which could not be determined in the fossil, is the fusion of ovular and wing vascular bundles to form a true ventral bundle (Sterling, 1966c). A vascular supply of five bundles (one dorsal, two wing, two ovular) to each carpel is the primitive condition among members of the Rosaceae (Sterling, 1953, 1964c 1966a, 1969; Cronquist, 1968). The three bundle condition found in most members of the Rosaceae has arisen secondarily by fusion of the ovular bundles to the wing bundles. This is unlike a primitive three bundle condition found in most other groups. It is unfortunate that the ovular bundles could not be traced into the receptacle, for the presence or absence of their fusion to wing bundles could strengthen the position of Paleorosa relative to the Quillajeae and Sorbarieae. The features described above for modern genera are summarized in Table 2 for comparison with those of Paleorosa.

It is apparent that all extant genera have been subject to some change and that the ancestor or "primitive type" is no longer living. The great similarity of floral structure among the more primitive genera with erect ovules and those with pendulous ovules within the Quillajeae and Sorbarieae suggests that this divergence, which distinctly divides the Rosaceae, occurred within the earliest members of the Rosaceae. It is not yet known which form the ancestor of the family would have had. Both erect and pendulous, paired

Table 2. Selected reproductive features of genera of the
tribes Maleae, Spiraeeae, Holodisceae, Ulmarieae,
Quilajeae, and Sorbarieae. (Information derived
from Sterling, 1964a,b,c, 1965a,b,c, 1966a,b,c)
Genera appear in the order by which they are
treated by Sterling.

[1]Ovular insertion

a - apical

b - basal

pl - many ovules

[2]Integumentary fusion

+ fused

- free

+(-) most species fused

-(+) most species free

[3]Intercarpellary fusion

+ carpels fused above level of ovular
insertion

(+) carpels slightly fused

- carpels free

0 single carpel involved

[4]Carpel to floral cup fusion

fraction of height through which
carpels are fused to the floral cup

+ fusion to level of ovular insertion

(+) slight fusion

- carpels free from floral cup

	Ovular Insertion[1]	Number of Carpels	Number of ovules per carpel	Integumentary Fusion[2]	Intercarpellary Fusion[3]	Carpel to Floral Cup Fusion[4]
Maloideae						
Maleae						
Crataegus	b	1-5	2	+-	+-	.5-1.0+
Hesperomeles	b	5	1	+-	+	.7-1.0+
Mespilus	b	5	2	+	+	1.0
Osteomeles	b	5	1	-(+)	+	1.0
Chamaemeles	b	1	2	+	0	.9
Cotoneaster	b	2-3	2	-	-	.5- .8
Dichotomanthes	b	1	2	-	0	0 or less
Pyracantha	b	5	2	+-	-	.3- .5
Amelanchier	b	2-5	1-2	-(+)	+	.4-1.0
Aronia	b	5	2	+-	+	.5- .8
Malacomeles	b	2-3	1	+-	-	.6- .9
Malus	b	3-5	2	-	+(-)	1.0+
Peraphyllum	b	2-3	2	-	-	1.0+
Pyrus	b	2.5	2	-	+-	.8-1.0+
Sorbus	b	3	2	+-	-	.6- .9
Photinia	b	1-3	2	+-	+	.3- .8
Heteromeles	b	2	2	-	-	.4
Eriobotrya	b	2	2	+-	+	.6-1.0+
Pourthiaea	b	2-3	2	+-	+	.5- .7
Raphiolepis	b	2	2-4	+	+	1.0+
Stranvaesia	b	5	2	+-	+	.7- .9
Chaenomeles	pl	4-5	16-36	+(-)	+	1.0+
Cydonia	pl	5	15-48	-	+-	1.0+
Docynia	pl,b	5-7	4-7	-	-	.6- .8

	Ovular Insertion[1]	Number of Carpels	Number of ovules per carpel	Integumentary Fusion[2]	Intercarpellary Fusion[3]	Carpel to Floral Cup Fusion[4]
Spiraeoideae						
Spiraeae						
Aruncus	a	3	3-7	+(-)	(+)	-
Kelseya	a	3-4	3-7	+	-	+
Luetkea	a	5	3-7	+	(+)	-
Petrophytum	a	5	2	+	(+)	-
Sibiraea	a	5	3-7	+	-	-
Spiraea	a	5	sev	+	(+)	-
Holodisceae						
Holodiscus	a	5-6	2	+	-(+)	-
Ulmarieae						
Ulmaria	a	5	2	+	(+)	-
Filipendula						
Quillajeae						
Exochorda	a	5	2	-	+	+
Lindleya	a	5	2	-	+	+
Quillaja	b	5	10-16	-	+	-(+)
Kageneckia	a,b	5	14-20	-	-	-
Vauquelinia	b	5	2	-(+)	+	+
Sorbarieae						
Chamaebatiaria	a	5	sev	-	+	+
Lyonothamnus	a,pl	2	4-6	-	(+)	+
Sorbaria	a	5	sev	+-	+	+
Gillenia	b,pl	5	2,sev	-	(+)	-
Spiraeanthus	b	4-5	2	+	+	+
Paleorosa	b	5	2	-	-	+

ovules are found in magnoliaceous and annonaceous genera
(Hutchinson, 1964).

Paleorosa seems to combine more primitive features than
any living member of the Rosaceae. It probably represents
an early group of rosaceous plants that preceded the
Quillajeae and Sorbarieae, and may signify the incipient
development of the Maloideae.

Rosaceous leaf remains appear frequently in the late
Tertiary but are much less common in sediments older than
Eocene (Kirchheimer, 1942). However, the accurate identi-
fication of many angiospermous fossils, particularly
Cretaceous and early Tertiary leaves, is now being questioned
(Dilcher, 1974). Remains of leaves and seeds assignable to
genera such as Amygdalus and Prunus from the Upper Cretaceous
and Eocene may support the theory that the Amygdaliodeae
was one of the earliest rosaceous lines to emerge (Sterling,
1966b; Robertson, 1974). Remains attributable to the other
three sub-families are apparently scarce in sediments older
than Oligocene. Paleorosa is one of the oldest known members
of the Rosaceae, and is presently the oldest known rosaceous
flower. Thus, it is the earliest well documented record of
rosaceous floral structure. If Paleorosa is an accurate
indicator of the state of floral development in the Rosaceae
during the Middle Eocene, then this is evidence that supports
the theory, mainly derived from floral anatomy of living
representatives, that the tribes Quillajeae and Sorbarieae
are, indeed, primitive.

Figs. 75 - 78.   *Paleorosa similkameenensis.* (a = anther;
                  b = bract; c = carpel; d = dorsal vascular
                  bundle; fc = floral cup; p = petal; pd =
                  pedicel; s = sepal; sy = style; vb = vas-
                  cular bundle in floral cup.)

Fig. 75.   Transverse section through the gynoecium
            showing the floral cup, five carpels, and
            two ovules per carpel. The obliqueness of
            the section shows one of the five carpels
            fused basally with the floral cup. The
            other four are sectioned above the point of
            fusion and are seen to be free. Note the
            vascular bundles of the floral cup. Those
            opposite carpels supply sepals, those alter-
            nating with carpels supply petals. Note also
            the dorsal bundle in each carpel. Pl122 I7
            X 41.

Fig. 76.   Longitudinal section of a flower in bud
            stage showing general features. Carpels do
            not appear in this section, but two styles
            are evident. Note the bract attached at the
            base of the pedicel. Pl123 B top9 X 38.

Fig. 77.   Longitudinal section of a flower in bud stage.
            The two large anthers were near maturity
            when permineralized and contain pollen grains.
            Pl118 E bot4 X 31.

Fig. 78.   Slightly oblique transverse section through
            the top of the floral cup showing alternate
            insertion of petals and sepals. Pl122 I9
            X 116.

75

76

77

78

Figs. 79 - 82. *Paleorosa similkameenensis.* (a = anther; co = connective; d = dorsal vascular bundle; f = filament; fu = funiculus; ii = inner integument; oi = outer integument; ps = pollen sac; sy = style; v = ventral vascular bundle; vs = ventral suture.)

Fig. 79.   Longitudinal section of a flower showing three anthers. The anther at the center shows the broad connective and attached pollen sacs. The anther at the left shows the dorsal attachment of the filament. Pl122 I16 X 35.

Fig. 80.   Oblique section showing several anthers in transverse section. Only the connective remains, the pollen sacs having decayed. Pl119 J bot8 X 34.

Fig. 81.   Oblique section through four carpels showing vasculature of carpels and ovules. Each carpel has two ventral bundles, a dorsal bundle, and a variable number of vegetative bundles. A single bundle is seen in each funiculus. Pl143 E bot15 X 38.

Fig. 82.   Section similar to that shown in Fig. 81. Inner and outer integuments are indicated. Vasculature as shown in Fig. 81 is also seen here. Note the ventral suture of each carpel. Pl143 E bot20 X 52.
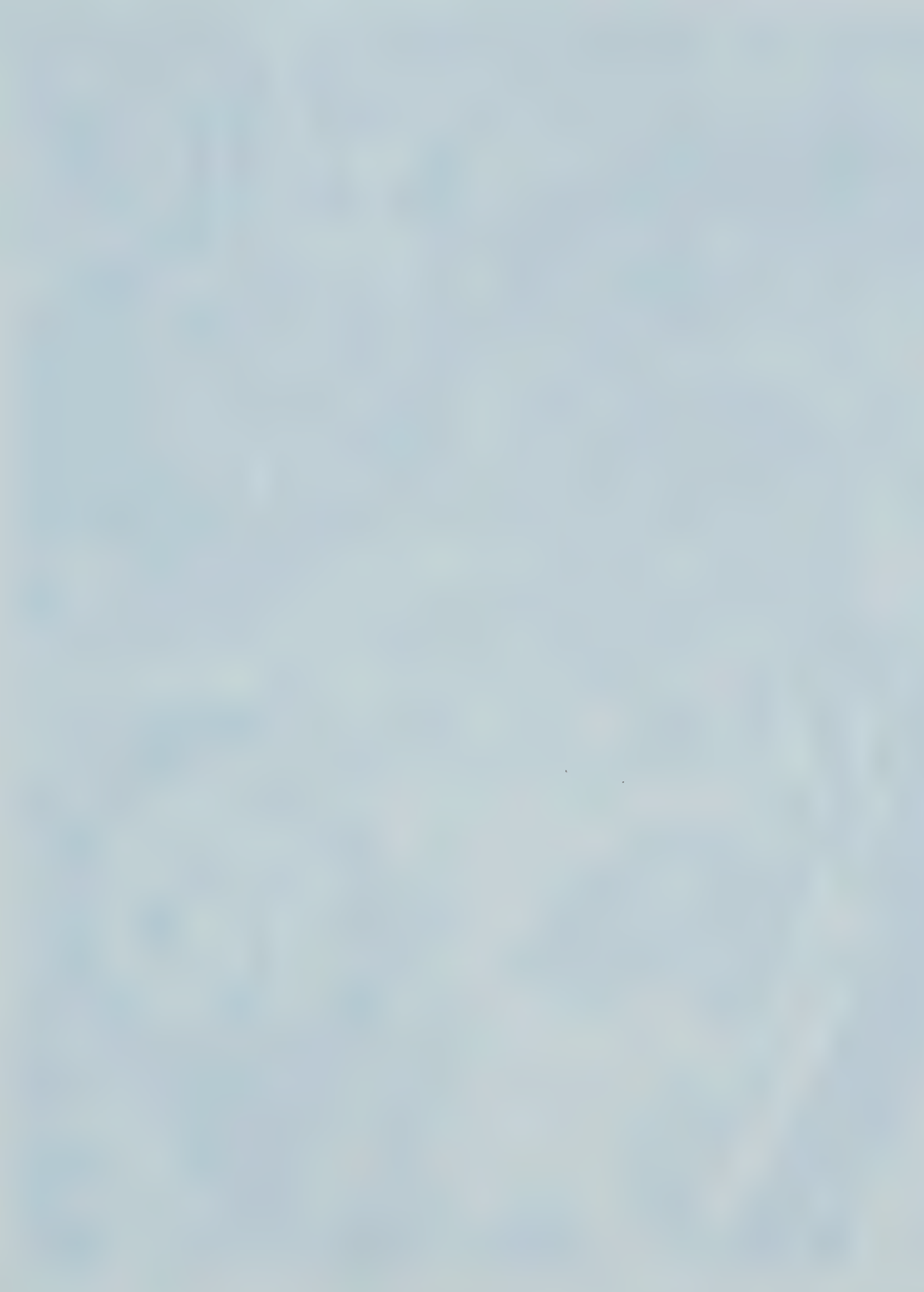
Figs. 83 - 87. *Paleorosa* *similkameenensis*. (a = anther;
c = carpel; d = dorsal vascular bundle;
fc = floral cup; h = hairs; p = petal; s =
sepal; se = septum between adjacent pollen
sacs; sy = style; vs = ventral suture.)

Fig. 83. Oblique section of a flower with well dev-
eloped carpels in addition to anthers.
Pl123 L2 19 X 32.

Fig. 84. Longitudinal section of a flower in bud
stage showing anthers and carpels. Note the
fusion of carpels to the floral cup and the
transverse section of the uppermost anther.
Pl119 J botl X 41.

Fig. 85. Oblique section showing a carpel containing
an ovule on the left and the lowest part of
the style of a second carpel on the right.
Note the hairs covering the surface of both
carpel and style. Pl143 E botll X 62.

Fig. 86. Oblique transverse section of two styles
showing the hollow center, dorsal bundle,
and ventral suture. Pl122 H bot22 X 120.

Fig. 87. Anthers of the flower in Fig. 77. showing
pollen grains. Note the septum which in-
completely divides pollen sacs. Pl118 E
bot4 X 105.
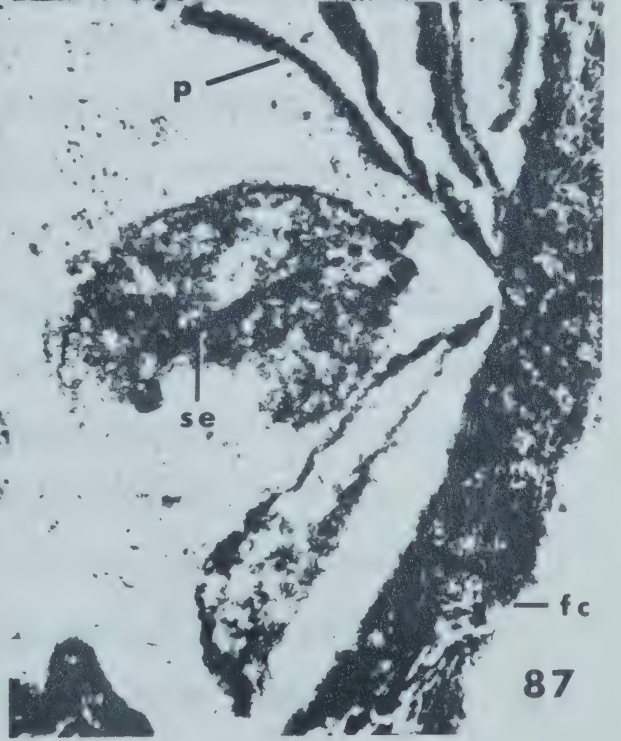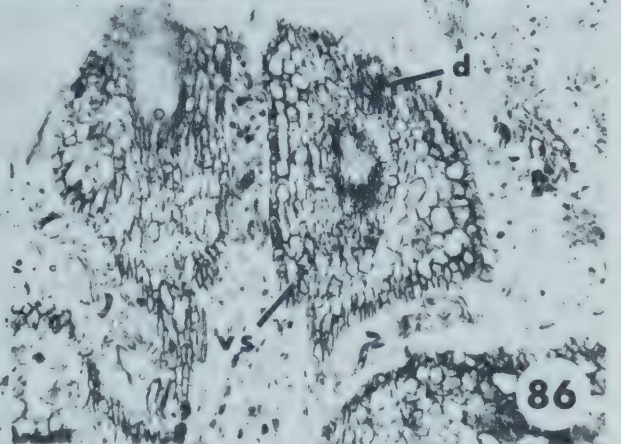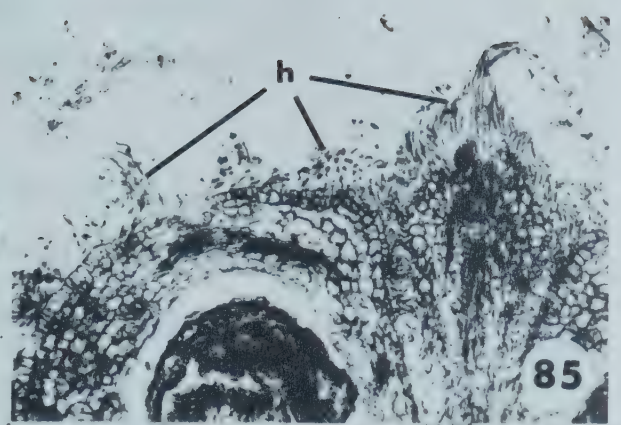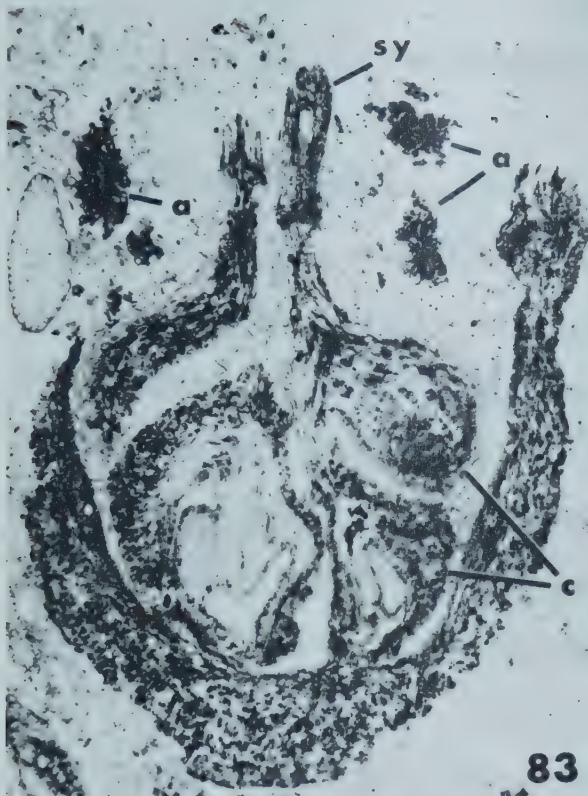
Order, Family: Incertae sedis

Eorhiza arnoldii (Figs. 88-98)

DESCRIPTION - Rhizomes and roots of this semiaquatic dicot
are found in the majority of chert layers, occasionally in
abundance, but usually as a minor component associated with
the remains of other angiosperms and Pinus. Leaves and
reproductive organs have not been found. Specimens of
Eorhiza arnoldii were described in some detail by Robison
and Person (1973), but the present study has allowed for
minor modification to their description.

Rhizomes are 2 - 3 cm in diameter and somewhat
flattened (Fig. 88). That this is the actual shape and not
a result of compression is shown by the lack of compaction
of cortical aerenchyma and pith cells. The pith is large
and solid, with a diameter of about one-half that of the
entire rhizome. Surrounding the pith are numerous endarch
primary xylem strands (Fig. 91). The secondary xylem is
up to 2.0 mm thick and is characterized by vessel elements
with oblique, scalariform end walls, scattered parenchyma
cells, and both uni- and multiseriate rays (Robison and
Person, 1973). The cortex is composed of an inner,
aerenchymatous zone and a thin, outer zone of solid
parenchyma. The uniseriate epidermis is without hairs.

Although leaves have not been found, remnants of
broad, clasping leaf bases are found attached to the
rhizomes. They are not restricted to any particular side

of the rhizome and appear to be produced in a regular
sequence (Fig. 89). The nature of this sequence has not
yet been determined. Several very large traces and numerous
small ones are found to pass through the cortex and into
each leaf base. Leaf trace origin must be studies in more
detail before a detailed description can be made. It
appears, however, that Eorhiza has multilacunar nodes.

Robison and Person (1973) were unable to determine the
nature of lateral branching. They reported the projection
of two branch traces into the cortex and the subsequent
formation of a vascular cylinder, presumably derived from
the two branch traces. As is seen in the series of Figures
93 - 97, branching is quite complex. A large number of
traces are given off and assembled to form the lateral
branch and a very large branch gap. Leaf traces are pro-
duced by the vascular cylinder before the branch has
departed. Wherever these departing branches were followed,
they were found to form a bud. Enclosing the apex are what
appear to be bud scales, for they do not appear to have any
kind of a distal, laminar structure (Figs. 97, 98). These
branches are borne on the lateral sides of the rhizome.

DISCUSSION - The function of these lateral branches is now
open to question. Robison and Person (1973) assumed that
their function was similar to that of the main rhizome, or
that the formation of these structures was a branching of
the rhizomatous system of the plant. Occasionally there are

near equal divisions in the rhizomes that resulted in two functional rhizomes. The lateral branches, however, are much smaller than the parent axis and appear quite frequently on the rhizome.

As yet, the only known appendages borne by the rhizomes, are the leaves and the lateral branches. Since Eorhiza must have produced a flowering axis, a suspicion arises as to the function of the lateral branches. It is my belief that these laterals were not destined to become rhizomatous, but that they developed into erect floral axes.

Robison and Person could not determine the taxonomic position of Eorhiza primarily due to the lack of knowledge of the structure of rhizomes of extant plants. Identification of this plant may have to await the discovery of reproductive structures. Numerous seeds and fruits, some of which may have been produced by Eorhiza, are found in association with the rhizome.

Figs. 88 - 89. *Eorhiza arnoldii.*   (lbr = lateral branch;
               lb = leaf base; r = root).

   Fig. 88.   Cross section of rhizome showing general
              features. Note the two lateral branches
              to the upper left and lower right and the
              adventitious roots. Pl111 D bot8 X 4.3.

   Fig. 89.   Oblique longitudinal section of a rhizome
              showing the attachment of several leaf bases.
              Pl143 E bot6 X 5.
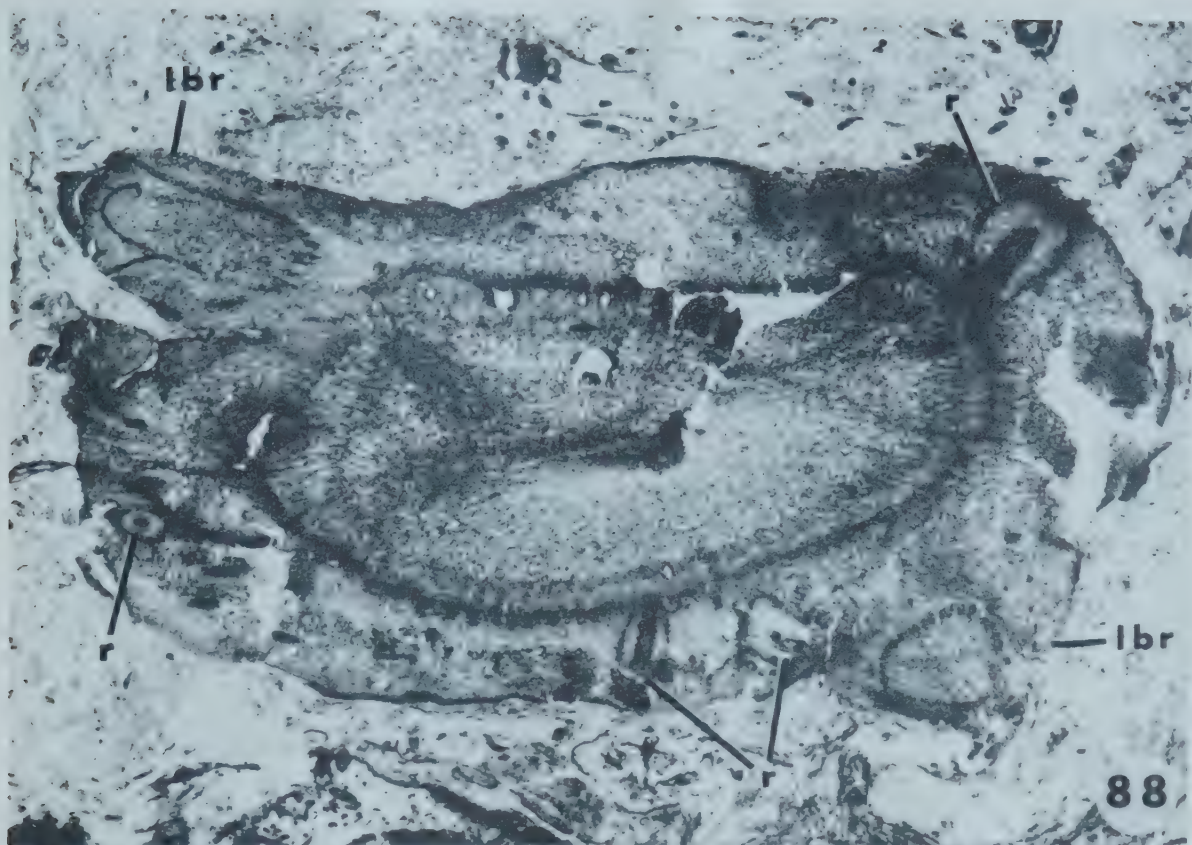
Figs. 90 - 92. Eorhiza arnoldii. (lr = lateral root;
                lt = leaf trace).

    Fig. 90. Cross section of a rhizome showing the de-
              parture of leaf traces. Note the lateral
              branch to the upper left. Pllll E top X 3.5.

    Fig. 91. Closeup of part of the vascular cylinder of
              the specimen shown in Fig. 90. Note the
              leaf traces, solid pith (left), aerenchyma-
              tous cortex, and secondary xylem. Pllll E
              top X 14.

    Fig. 92. Cross and longitudinal sections of roots
              of Eorhiza. Note the aerenchymatous cortex
              and the production of lateral roots. Pl224
              B top X 9.
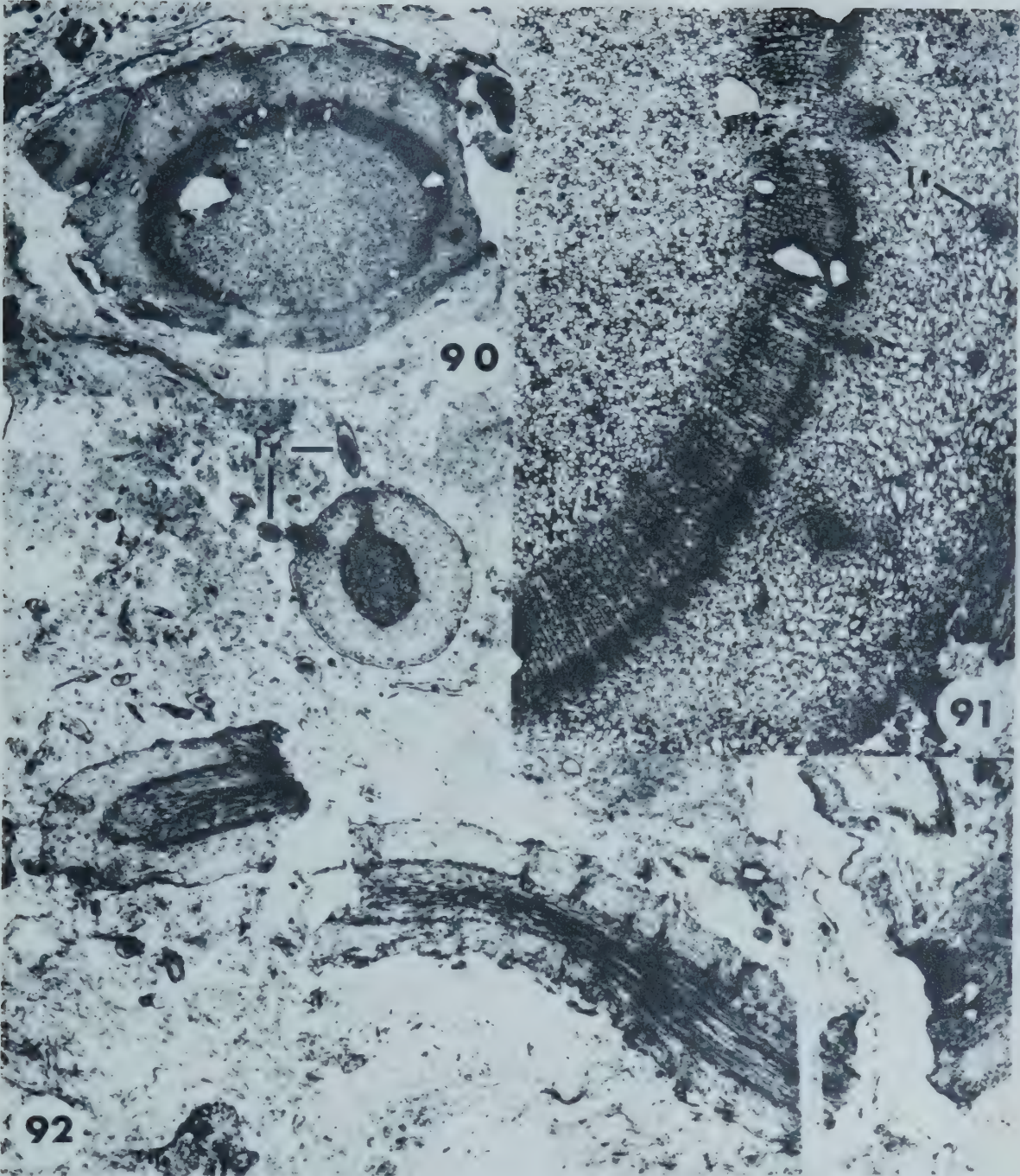
Figs. 93 - 97. *Eorhiza* arnoldii. Serial cross sections of
               a rhizome showing the structure of a lateral
               branch. (bt = branch trace; bg = branch gap;
               lf = leaf; lt = leaf trace; p = pith; r =
               root; 2°X = secondary xylem).

Fig. 93.   Several branch traces can be seen passing
           through the cortex of the parent rhizome.
           Note leaf traces present in the cortex of the
           lateral branch. The structure left of center
           is a root. Pl111 D bot35 X 6.

Fig. 94.   Note the branch gap. Pl111 D bot30 X 6.

Fig. 95.   Note that interfascicular secondary develop-
           ment has formed a complete vascular cylinder
           at a short distance from the vascular tissue
           of the rhizome. Pl111 D bot21 X 6.

Fig. 96.   Pl111 D bot8 X 6.

Fig. 97.   Lateral branch with apical scales or young
           leaves. Pl111 D bot1 X 6.

Fig. 98.   *Eorhiza* arnoldii. Oblique section of the
              distal portion of a lateral branch showing
              their bud-like structure. Pl139 C top4 X 10.

93

lt

bt

r

P

2°x

94

bg

95

96

97

lf

98

lf
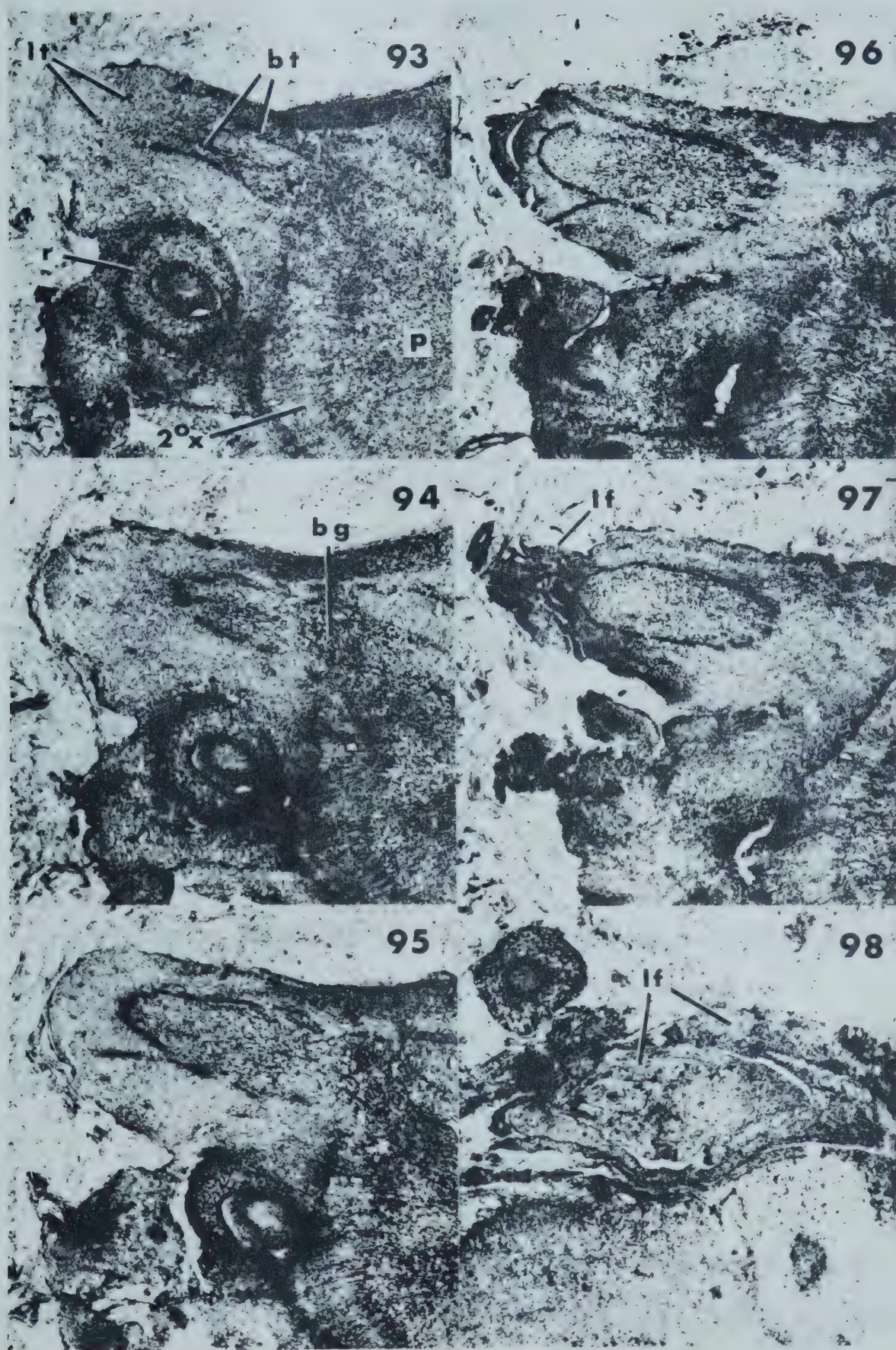
Incertae sedis

The specimens shown in Figures 99 - 107 have been
selected from a large number of as yet unidentified fruits,
seeds, and leaf remains. Associated with these organs are
several types of dicotyledonous foliage and woody and
herbaceous stems. No attempt has yet been made to determine
affinities of these plant parts. They will be discussed
separately by figure number.

Fig. 99

This fruit is approximately 1 cm in diameter. There
are no seeds remaining in any of the five locules, but the
large placenta present in each probably bore numerous seeds.
This fruit is commonly found in association with Eorhiza
arnoldii.

Fig. 100

Numerous seeds are preserved within this fruit. There
appears to be four locules, but the septa are not well
defined. The dispersed seeds of this type of fruit are
perhaps the most common type of seed found in the chert.

Fig. 101

The seeds of this fruit appear to have aborted prior
to fossilization, although their structure may be an artifact

of preservation. The small seeds of this fruit are about the same size as those of Fig. 100, and are also very common.

Fig. 102

This type of foliage is the most common dicotyledonous foliage present in the chert. An association with any particular reproductive structure has not yet been established.

Figs. 103 - 107

These seeds show good structural preservation of the seed coat, but embryos have not been recognized. In many cases, cellular tissue is found within them, but no structure can be seen. It is possible that this tissue is endosperm.

Figs. 99 - 101. Incertae sedis. Fruits found in the Ash-
                 nola chert.
     Fig. 99.   Five locular fruit in a post-dispersal
                 state. Pl126 G X 6.

     Fig. 100.   Four(?) locular fruit containing numerous
                 seeds. Pl142 D bot X 14.

     Fig. 101.   Fruit with abortive or poorly preserved
                 seeds. Pl138 H X 14.

Fig. 102.   Incertae sedis. Dicotyledonous foliage.
                 Pl060 F top.

Figs. 103 - 107. Incertae sedis. Some of the many types of
                 unidentified seeds found in the chert.

     Fig. 103.   Pl230 D top X 6.

     Fig. 104.   Pl060 F bot X 10.

     Fig. 105.   Pl229 D X 11.

     Fig. 106.   Pl135 C top X 10.

     Fig. 107.   1060 G top X 14.
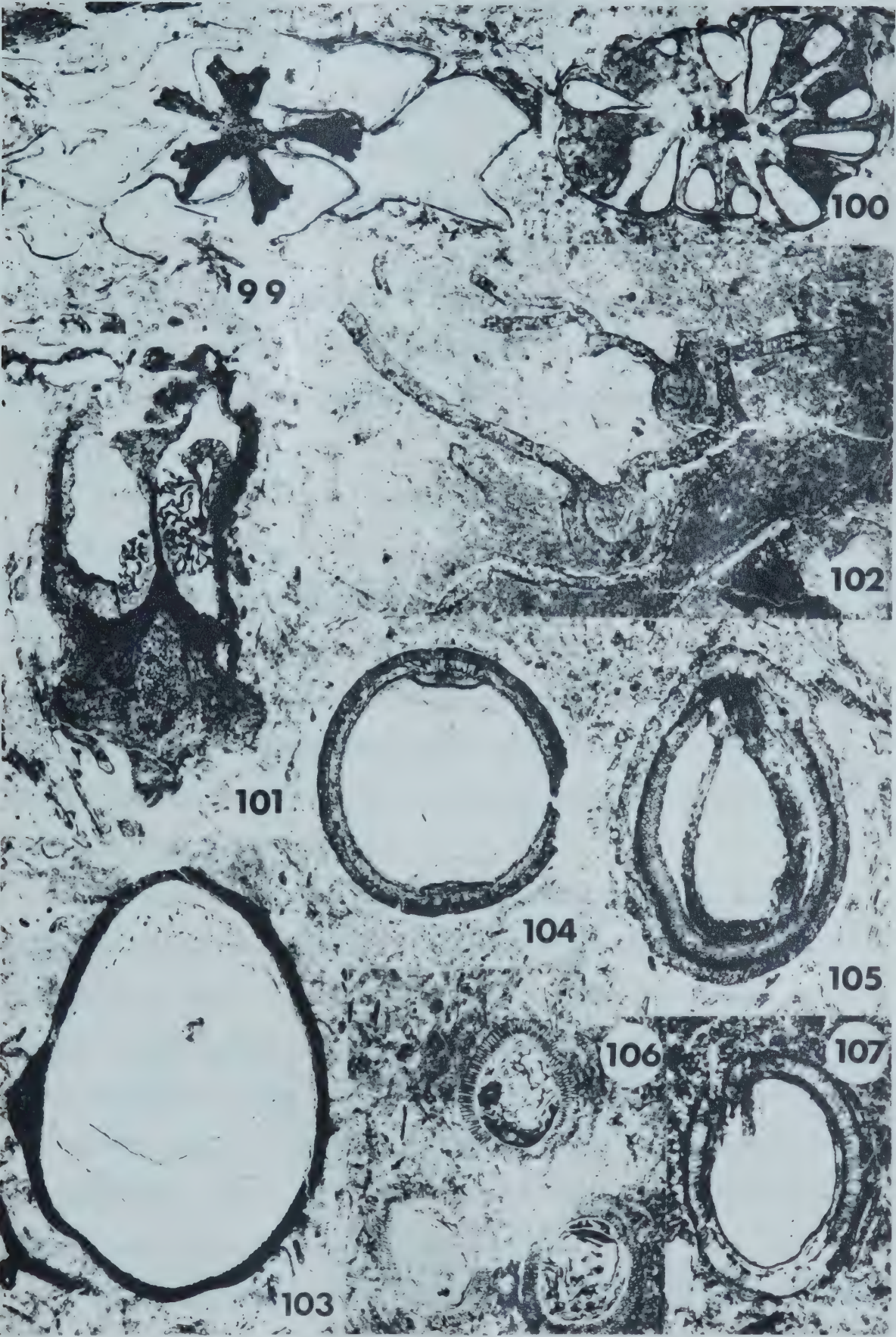
Class: Angiospermopsida

Sub-Class: Monocotyledonae

Order: Palmales

Family: Palmae

Incertae sedis (Figs. 108-117)

DESCRIPTION - The remains of petioles, laminae, and roots
of this palm are found in abundance in some of the chert
layers. No stems or reproductive structures have been
identified.

Petioles are 1 - 3 cm in diameter and are somewhat
aerenchymatous (Figs. 108, 113). Both vascular and fiber
bundles are scattered throughout the ground tissue (Fig. 110).
Vascular bundles possess a single, large metaxylem vessel
and a number of smaller vessels and tracheids. Phloem is
divided into two areas by a zone of fibers. A fibrous
bundle sheath encloses the vascular tissue except at points
opposite the large vessel.

Midribs and leaf laminae are found in association
with the petioles, but have not yet been found attached
(Figs. 111, 112). Midribs have more than one (usually
three) large vascular bundles at the center and many smaller,
fiber bundles at the periphery. The vascular bundles have
two to five large vessels, differing from those found in
the petioles. A zone of expansion tissue is found between
the points of attachment of the lamina.

Roots are found in a wide range of size, but all show

the same basic features. The pith of larger roots is generally absent, but is seen to be parenchymatous in smaller roots. A ring of very large metaxylem vessels is found adjacent to the pith (Fig. 114). Trachery element size gradually decreases toward the endodermis, where the numerous protoxylem points can be observed. Cells of the endodermis are thickened on the inner, radial and horizontal walls, while the outer wall is relatively thin. The root cortex is aerenchymatous (Fig. 116), but poor preservation often obscures this.

DISCUSSION - Although these organs have not been found attached, they are in very close association and there appears to be only one type of each organ present. This leads to speculation that they represent a single species. The roots have a structure that appears fairly commonly in palms, but the petioles and especially the midribs are useful in identifying the fossil.

Tomlinson (1961, p. 40) divided the palms into two major groups, among other characteristics, on the basis of midrib anatomy:

"(i) In the fan-palms of the Sabaloid and Borassoid groups, but not Lepidocaryum and Mauritia of the Lepidocaryoid palms, the central ground parenchyma contains one or more large vascular bundles which are like the large veins of the lamina and, with few exceptions, are not confluent ... . Adaxial and abaxial ribs differ mainly in size.

(ii) In all other palms except Phoenix, i.e. the feather-palms together with Lepidocaryum and Mauritia, there is a complete fibrous cylinder

occupying most of the rib and enclosing a central
colourless ground parenchyma ... . Within this
central tissue is a larger abaxial vascular bundle,
the phloem of which may be rather diffuse, together
with smaller vascular bundles mostly situated
adaxially and often inversely orientated, and even
isolated phloem strands. These smaller bundles are
often embedded in the peripheral fibrous tissue, as
in many Lepidocaryoid palms."

The presence of more than one large bundle and the

lack of a fibrous cylinder clearly places the fossil in

the fan-palms.

An additional characteristic of fan-palms is the

presence of a single mass of expansion tissue in the fold

of the midrib. In the feather palms, there are two bands

of expansion cells, one on each side of the midrib.

A distinction between Sabaloid and Borassoid palms

was made by Tomlinson (1961) on the nature of the phloem

in the vascular bundles. Borassoid palms have a single

mass of phloem in each bundle, while the bundles of

Sabaloid palms typically have two phloem zones separated

by a fibrous partition. There are two phloem zones found

in the vascular bundles of both fossil petioles and midribs.

This characteristic is indistinct in Fig. 110 and 112, but

in less well preserved specimens the phloem has decayed

prior to permineralization and has left behind two

cavities separated by the fibrous partition.

On the basis of this evidence, then, the fossil is

referred to the Sabaloid palms. More accurate identification

must await further study.

This is the first report of palm remains from the

Allenby Formation. The presence of this palm indicates a
very warm temperate to subtropical climate in the Princeton
area during Allenby time. The aerenchymatous nature of
both petioles and roots is reminiscent of the structure of
Dennstaedtiopsis aerenchymata, unidentified fern B, and
Eorhiza arnoldii and is further evidence for a marshy
habitat at the Ashnola locality at the time of formation
of the chert layers.

Fig. 108 - 112. Palmae. Incertae sedis. Petioles and
                 midribs. (bs = fibrous bundle sheaths;
                 et = expansion tissue; fb = fiber bundle;
                 l = leaf lamina, mv = metaxylem vessel;
                 ph = phloem; x = xylem).

     Fig. 108.   Cross section of palm petiole showing
                 general features. Pl124 G bot X 3.

     Fig. 109.   Cross section of a small petiole.Pl171 B bot X 3.5.

     Fig. 110.   Closeup of vascular bundles and ground
                 tissue of a petiole. The ground tissue is
                 aerenchymatous and contains numerous
                 fiber bundles. The vascular bundles have
                 a single, large metaxylem vessel and several
                 smaller cells of the metaxylem and protoxylem.
                 Phloem is divided into two zones by a band
                 of fibers. The fibrous bundle sheath is
                 discontinuous opposite the metaxylem vessel.
                 Note the tyloses within the vessels. Pl165
                 F2 bot X 71.

     Fig. 111.   Cross sections of two palm midribs.Pl171 C
                 top X 11.

     Fig. 112.   Closeup of a midrib showing three large,
                 vascular bundles at the center of the
                 midrib and several smaller, fiber bundles
                 at the periphery. Note also the mass of
                 expansion tissue and the remnants of the
                 lamina. Pl171 B bot X 68.

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Fig. 113.   Palmae, Incertae sedis. Longitudinal
                    section of a petiole. Note the aerenchy-
                    matous ground tissue. P1165 D top X 9.

Figs. 114 - 117.   Palmae, Incertae sedis. Roots (lr -
                    lateral root, mv = metaxylem vessel).

    Fig. 114.   Cross section of a large root. The vas-
                    cular tissue is composed of a ring of
                    very large vessels interior to smaller
                    vessels and tracheids. A zone of scler-
                    enchyma surrounds the stele. The cortex
                    is primarily aerenchymatous. The pith
                    has not been preserved. P1064 C top X 11.

    Fig. 115.   Cross section of a large root shown giving
                    rise to a smaller, lateral root. P1165 F2
                    bot X 6.

    Fig. 116.   Cross section of a small root showing the
                    aerenchymatous structure of the cortex.
                    P1230 B top X 25.

    Fig. 117.   Cross section of a very small root. P1171
                    E top X 44.
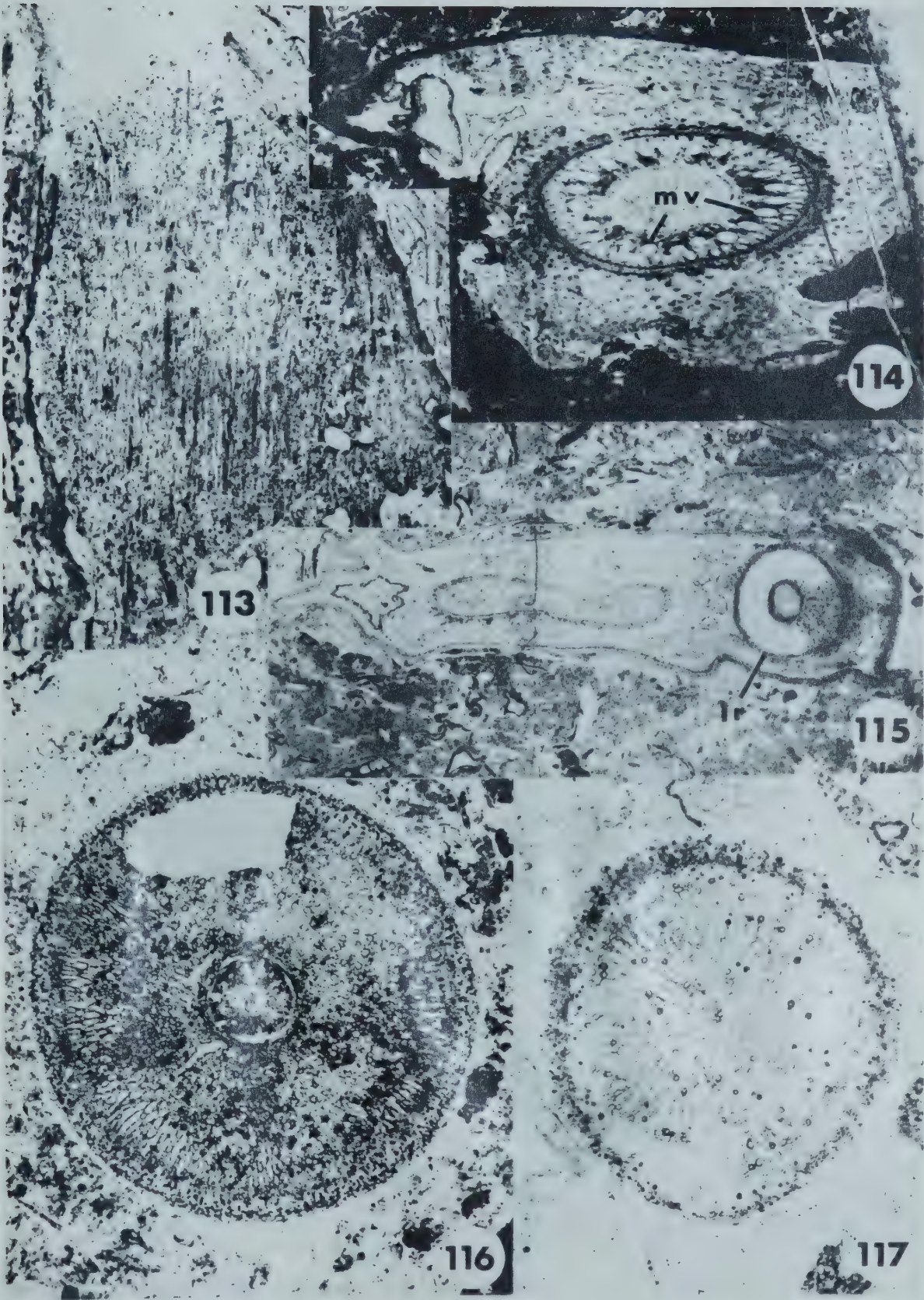
CHAPTER 5

DISCUSSION

The flora of the Ashnola locality shows an interesting combination of both subtropical and temperate elements. Pinus and Metasequoia indicate a temperate climate. Members of the Maloideae are principally temperate and so, presumably, was Paleorosa. Sabaloid palms, however, are more indicative of a subtropical to very warm temperate environment. In the Clarno Formation of Oregon Dennstaedtiopsis aerenchymata is closely associated with Acrostichum preaureum (Arnold and Daugherty, 1964), the living equivalents of which are found in tropical mangrove swamps. An investigation of climatic conditions present in western North America during the Eocene may help to explain the composition of the Ashnola flora.

Climatic Conditions During the Middle Eocene -

Following a deterioration in world climate at the end of the Cretaceous, there was a warming trend during the Paleocene which reached an optimum during the Eocene. Following this there was again a cooling extending through the Oligocene, a slight recovery during the Miocene, and a rapid deterioration through the late Miocene and the Pliocene which led eventually to the Pleistocene Glaciation (Brooks, 1951). The climatic optimum of the Eocene appears to coincide with the deposition of the Allenby Formation, and at this time floras reached their maximum northern extent.

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Although drift of the continents has altered the position of the North Pole relative to North America, latitudinal positions occupied at the present will be retained in discussing the past. This is done because estimations of paleoclimate and paleoecology, as well as correlations of floras and faunas, are discussed in reference to geographical localities which have not changed position relative to one another.

Durham (1950) indicates that the marine climate at 49° latitude was subtropical to tropical during the Eocene. This warm ocean would contribute to a warm and moist coastal climate. The Ashnola locality now lies in the rain shadow of the Cascade Mountains, but this range was not present during the early Tertiary (Dott and Batten, 1971). Thus, the climate at the Ashnola locality could have been under oceanic influence, although just how much influence could be felt at more than 100 miles from the coast is debatable.

Chaney (1949a) recognizes two distinct types of older Tertiary floras and describes them as follows:

"The first of these is a subtropical assemblage made up predominantly of broad-leafed evergreen angiosperms whose living equivalents occupy regions in which freezing temperatures are seldom if ever recorded; palms and cycads are represented by a few species which may be abundant; conifers are rare or absent. This forest occupied a zone from California north to Washington on the Pacific Coast, and from New Mexico to Colorado in the interior. Because of its apparent origin in low American latitudes, it is known as the Neotropical-Tertiary Flora. The second major group is a temperate assemblage made up predominantly of broad-leafed deciduous angiosperms, and of conifers both deciduous and evergreen; palms and cycads have not been recorded. This forest

occupied a zone in Alaska northward beyond the Arctic
Circle, extending into the Mackenzie Basin of Canada.
Evidence of distribution farther eastward has been
destroyed by Pleistocene glaciation, but its former
occurrence across northern Canada is suggested by
the records of similar plant fossils in the Eocene
rocks of Greenland, Spitzbergen, and arctic Siberia.
Because of its wide development at high northern
latitudes, this assemblage is known as the Arcto-
Tertiary Flora. It lived in a region of summer
rainfall and winter cold, as judged by the habits
of related living trees."

Chaney goes on to say that oceanic influence allowed some

of the southern forms to exist on the Pacific coast as far

north as Alaska. Inland, however, typical Arcto-Tertiary

forms would be found. Although the concept of Neotropical-

and Arcto-Tertiary geofloras has met with well-founded

opposition (Wolfe, 1969), a diminuition of the tropical

elements northward would be expected to have occurred in

the Eocene in a similar way as occurs at present.

The Ashnola locality is located in an area which may

be considered transitional. It is far enough inland that

the ameliorative effect of the ocean would be somewhat

reduced, but probably not far enough north to be subject

to severe frost. Of this transitional zone Chaney (1949a)

says:

"In the areas between these two major zones of
vegetation there is a record of a forest made up
of largely temperate trees. Living with them were
several members of the subtropical forest which
appear to have made their way northward beyond the
range of occurrence of most of their associates,
during the relatively mild days of the early Tertiary.
This ecotone is best developed in southeastern
Alaska, on Kupreanof Island at latitude 56 to 57
degrees north. Here is the typical Kenai flora,
as described by Hollick (1936) from 55 localities
in Alaska, including such temperate trees as redwood

(Metasequoia), katsura (Cercidiphyllum), birch (Betula), alder (Alnus), hazel (Corylus), hornbeam (Carpinus), chestnut (Castanea), oak (Quercus) and elm (Ulmus). Immediately associated, and often on the same slabs of rock, are the leaf impressions of several members of the Neotropical-Tertiary Flora; these include two genera of cycads (Dioon and Ceratozamia), a fan palm (Flabellaria), laurels of the avocada (Persea) and lance-wood (Ocotea) type, magnolia (Magnolia) and catmon (Dillenia)."

Chaney (1949a) describes this zone as extending along the northern Pacific coast and stretching eastward from southern British Columbia to southern Saskatchewan, and to Montana and North Dakota. The flora of the Ashnola locality, which is contained within this transitional zone, coincides with the proposed vegetation and climate of the region.

Altitudinal Effects on Vegetation in the Princeton Area During the Middle Eocene -

In addition to latitude having an effect upon vegetation, it is also expected that altitude should bring about a response in floral composition (Chaney, 1949a; Axelrod, 1966). Axelrod (1966) gives an estimation of 750 meters for the elevation of the Princeton area during the Eocene, but does not give his basis for such a value. He likely followed Rouse (1962) who believed that the relationships between the Burrard and Allenby floras indicate a similar altitudinal difference as exists today.

Uplift of part of the Cordillera including the Princeton area during the formation of the Rocky Mountains is believed to have been responsible for the severe erosion of the Paleozoic rocks of the area (Dott and Batten, 1971).

It was previously noted that local subsidence during the Eocene most probably initiated deposition in the vicinity of Princeton. It is conceivable, then, that much of south central British Columbia could have had an elevation close to that proposed by Rouse and Axelrod. The basins formed by subsidence were possibly much lower than the surrounding hills, for they are filled with great thicknesses (2500 meters at Princeton) of basically coarse sediments and volcanics.

Although the elevation of the Ashnola locality could not have posed hardships on the vegetation, for palms are abundant, different floral assemblages may have existed at higher altitudes in other parts of the Princeton basin and contributed to misinterpretations of the age of the sediments.

Comparison of the Ashnola Locality with Other Localities of the Allenby Formation -

A great deal of difficulty exists in comparing per-mineralized with compressed plants. While leaves are the most common and easily recognized element in a compression flora, they are of very little use in a permineralized state, where laminar shape is almost impossible to determine. Likewise, anatomical detail of woods and reproductive organs, which is so important in a permineralization flora, is not applicable to compressed plants.

Since evidence for specific comparisons of plants of the Ashnola chert with other localities is, therefore, lacking, only very general comparisons are possible.

(For lists of fossil plants from the Allenby Formation, see Dawson, 1890; Penhallow, 1908; Arnold, 1955). Some of the Ashnola plants such as Eorhiza, palms, and ferns have not been reported from other localities of the basin, but this may be due to the unusual conditions of fossilization at the Ashnola locality. Both Metasequoia and Pinus are found in other localities (Arnold, 1955). Miller (1973) attempted to link Pinus similkameenensis with P. latahensis of P. tulameenensis, two five-needle pines from the Allenby Formation, but found differences in size too great. Dicotyledonous remains have yet to be dealt with. Distinct growth rings found in the various types of ring-porous woods indicate a winter dormancy that was probably accompanied by a deciduous habit, although growth rings may be produced by drying as well as cold. Forests represented by other localities are basically deciduous.

The temperate aspect of the Ashnola flora appears similar to other floras of the Allenby Formation, although evidence is yet incomplete. A major difference is in the presence of more tropical elements at Ashnola, for this is the first report of palms in the Princeton area. I believe that these palms are an indicator of a rather mild climate in the area, but they could be the result of an unique microclimate possibly created by the warm mineral springs responsible for periodic permineralization. It is possible that the palms were able to withstand cool temperatures and do not signify a warm climate. However, in consideration

of the ranges of modern palms and the nature of the plants associated with fossil palms, this is unlikely. It is the temperate aspect of the composite flora, which was compared with temperate floras typical of late Tertiary deposits, of the Allenby Formation that has resulted in misinterpretations of the age of these sediments.

Discrepancies in Age Determinations of the Allenby Formation - Megafossil evidence led early investigators to believe that the Allenby Formation was of late Tertiary age (see Ashnola Locality - Age). Some recent work tends to support this as well (Chandrasekharam, 1975). In light of an established Middle Eocene age for the deposits, reasons for these contradictory determinations have been sought:
1) The inclusion of younger fossils in collections - An unconformity within the Allenby Formation would allow for the presence of younger material which could affect interpretations. Although no unconformities have been recognized within the Allenby Formation (Hills, 1965a), late Tertiary fossiliferous sediments that overlay part of the Princeton basin have been recognized by Mathews and Rouse (1963). If fossils from these deposits were included in early collections, as Mathews and Rouse suggest, confusion would result. However, localities exploited by the early investigators were primarily in the southern and western portions of the basin, while late Tertiary deposits were found only in the northern and eastern areas. In my opinion it is unlikely that a significant number of fossils from the younger

sediments would have been included in the early collections.

The relationships of the locality being worked on by Chandrasekharam (1975) to the Allenby Formation is still in question. The material is most certainly late Miocene, but is unlike other collections from the Allenby Formation. The material is found at the northern limits of the basin and is apparently quite high in the sequence. The nearby hills are capped by late Tertiary deposits, and it is my belief that this material has slumped from the late Tertiary beds and is now being confused with the older Tertiary sediments of the Allenby Formation.

2) The misinterpretation of floral assemblages - If it is assumed that younger material did not accompany early collections, a misinterpretation of the data is the cause of the conflicting ages. The introduction of temperate forms such as Pinus, Picea, Abies, Acer, and Betula (Arnold, 1955) could have been caused by:

a) The occurrence of brief climatic deterioration during the Eocene, which has been proposed by Brooks (1951), could have changed the aspect of the flora during Allenby time (Rouse, 1962). Hills (1965b) and Boneham (1968) found palynological evidence for zonation within the Allenby Formation. Boneham (1968, p. 34) suggests that:

> "It is possible that in the sediments below the
> Princeton-Black Seam the subtropical components of
> the flora are greater than above the Princeton-
> Black Seam. If such is the case, and it is not
> possible to say at this time due to a lack of data,
> then the Allenby Formation contains a record of
> changing climates which is worth further investigation."

Whether this apparent zonation is due to a climatic change or to some other physical change in the environment in the basin is open to question. The Ashnola locality is 600 meters above the Princeton-Black Seam and has at least one subtropical element, a sabaloid palm, which is very abundant.

b) The presence of a combination of subtropical to temperate forms, as is well shown by the Ashnola locality, could be a result of the mixing of northern and southern floras in a transitional zone.

c) Plant parts from floral assemblages at high altitudes could have been transported into the basin and then influence assemblages at various localities in the basin.

Some of the early age determinations were taken from comparisons of the Allenby flora with floras of other presumed late Tertiary formations which have since proved to be much older. Bell (in Rice, 1947) found similarities between the Allenby and Kitsilano floras, both of which he believed to be Oligocene. Arnold (1955) felt that the Allenby flora resembled the Republic flora, which he believed Oligocene. Since that time, the Kitsilano Formation has been found to be Middle Eocene (Rouse, 1962) and the Republic, latest Paleocene (Axelrod, 1966). Indeed, our understanding of Cretaceous and Tertiary floras has undergone a dramatic change with new approaches to the identification and interpretation of particularly angiosperm

fossil remains (Hickey, 1973; Dilcher, 1974). The cool temperate forms present in the Allenby flora have misled investigators in the past into believing in a later Tertiary age. However, I expect that a thorough reinvestigation will reveal a definitely early Tertiary, although somewhat temperate, assemblage.

Summary of Environmental Conditions at the Ashnola Locality During the Middle Eocene -

The Ashnola locality was described as the remains of an ancient marsh or bog of limited extent (see Ashnola Locality - Formation). Many plant organs have been preserved in situ (Dennstaedtiopsis, Eorhiza, palms) and show adaptations to an aquatic or semiaquatic habitat (aerenchyma).

If an observer were present at the Ashnola locality during the Middle Eocene, he would probably find himself in a small marsh, perhaps no larger than a few acres, on a valley floor. The water of the marsh would not be deep, and most of the area would be covered by hummocky vegetation including Dennstaedtiopsis aerenchymata and Eorhiza arnoldii. Immediately surrounding the marsh would be a dense forest of Metasequoia, Pinus, and fan palms. The undergrowth would include ferns and Paleorosa similkameenensis. The forest of the surrounding hills may have had a more conspicuous deciduous element and palms would be absent. The climate, which could be termed subtropical to warm temperate, would be quite warm and moist, with winter frost rare or

absent.

Future Possibilities of the Ashnola Locality -

The plants described in this thesis are a selection
of the best known representative forms found in the Ashnola
chert. Thus, the actual diversity of the flora is much
greater than has been presented here. Among Tertiary
permineralization localities, this diversity is rivaled
only by that found at Mohgaon Kalan in the Deccan Inter-
trappean Series of India. However, the plants found at
Mohgaon Kalan and at Ashnola are not similar. Few specimens
have been reported from other Tertiary permineralization
localities.

The Ashnola locality, then, presents an opportunity
to study early Tertiary plant structure and reproductive
mechanisms in a way not previously possible in North
America. This thesis has served to reveal the diversity of
the Ashnola flora and to provide a detailed description on
a single member of the flora, Paleorosa similkameenensis.
Many other plants, including Metasequoia, palms, ferns, and
the numerous dicotyledons, await study. Paleorosa, Pinus
arnoldii, and Pinus similkameenensis, which are the only
well-described plants from the chert, have already provided
valuable information on evolution within the Rosaceae and
Pinaceae. It is quite possible, then, that an investigation
of other forms will provide similar insights into evolution
within other groups. In view of the great potential of the
Ashnola locality, continued research on this material should

be considered as high priority in the field of Cenozoic
plant development and evolution.

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